ECOLOGY AND TAXONOMY OF ALPINE ALGAE, MT PHILISTINE, ARTHUR'S PASS NATIONAL PARK, NEW ZEALAND

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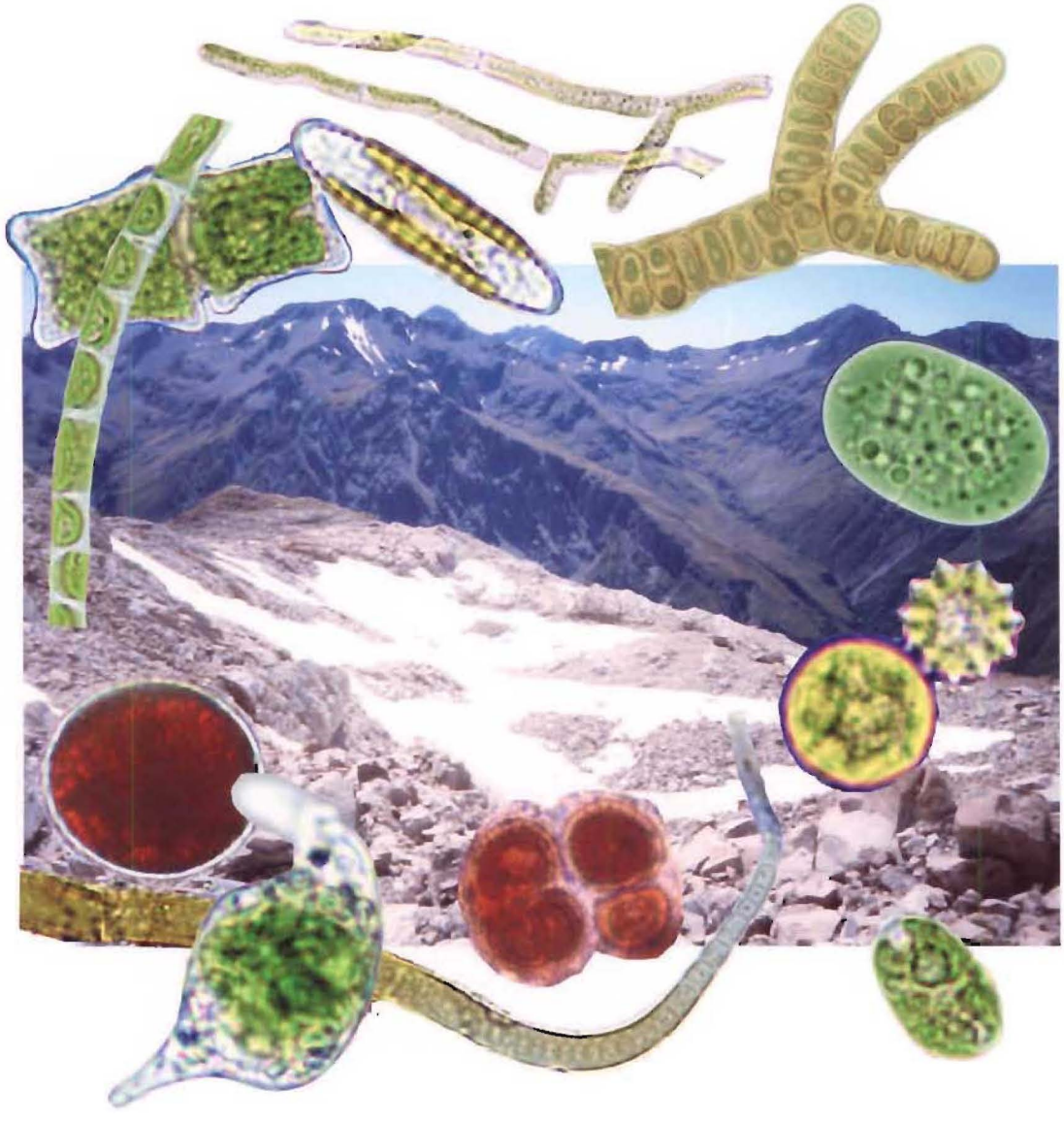

"... geographical exploration means more than the discovery and survey of a country; even a well-mapped area may be *terra incognita* to the botanist, the geologist, the zoologist, the archaeologist. Start, with a spark of interest, to look into the matter, and your head will soon begin to reel with the mass of fascinating problems crying out for investigation. It is a virulent bug, this desire to see around the next corner. An energetic lifetime spent in the pursuit will leave you as far from complete satisfaction as you were at the start."

Eric Shipton, *Upon That Mountain*

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ABSTRACT

At least 67 distinct algal taxa occur in the alpine basins of Mt Philistine, Arthur's Pass National Park. This flora differs from others reported in alpine and polar regions. Nine species of snow algae were found, none of which appear to grow in other habitats, and at least 6 of which are new records for New Zealand. An abundance of other algae are present, including cf. *Gloeocapsa*, *Cyanothece aeruginosa*, *Fischerella* sp., and *Myrmecia* cf. *irregularis*, which are particularly widely distributed throughout different habitats on the site. Certain other taxa are common in selected habitats, such as cf. *Ammatoidea* in some pools and *Chlainomonas kolii* in snow on the surface of an alpine tarn.

Distinct assemblages of algae occur in snow and associated with the moss *Andreaea mutabilis*. Assemblages in pools, soils, mineral fines, on rock surfaces, and associated with vascular plants are not distinguishable, which may reflect the shortcomings of using presence/absence data as the basis for ordinations.

The complete life-cycle of the enigmatic *C. kolii* is still not understood. This alga has previously been found only in snow beneath forest in North America, where it is generally exposed to much lower light intensity and higher nutrient levels than in alpine New Zealand. However, *C. kolii* on Mt Philistine grows during prolonged rainstorms, when liquid water content increases, light intensity decreases and freezing at night is absent. Timing of the bloom each year appears to be related to the amount of snow deposited during the previous winter.

Snow algae resting cysts are deposited by retreating snow onto underlying substrata on the site. However, their ultimate fate is unknown. Many algae are lofted and dispersed elsewhere, including onto snow from other habitats. An unidentified snow algal cyst (possibly *Chlamydomonas* sp.) is a small component of the aerobiota. *C. kolii* has not been found in these samples. The cyanophytes *Fischerella* sp. and cf. *Gloeocapsa* dominate the aerobiota. Collection of air-borne algae illustrates the problem of distinguishing wind-deposited propagules from active algae in a given habitat, especially those organisms requiring cultures for their detection and identification. Temporal variation of cultured organisms from aerobiota suggests that their growth periods are distinct from many of those absent from cultures. This is a further factor reducing the resolution of ordination techniques for analysis of distribution patterns.

CHAPTER 1.
GENERAL INTRODUCTION

1.1. Focus of this study

Taxonomy and ecology of alpine algae in the Southern Alps of New Zealand were intensively investigated at a single site. Of primary interest were the following:

- Which organisms make up the algal flora of the site?
- How are these organisms distributed among different habitats?
- What conditions are important for growth of snow algae on the site?
- How are algae dispersed between habitats?

1.2. Prior research on alpine algae in New Zealand

Snow algae, which cause visible colouration of snowfields, are the most commonly noted algae in alpine areas of New Zealand. Visible blooms have been reported from many mountain areas of the South Island and from Tongariro National Park in the North Island (Thomas and Broady 1997). However, algae occupy many other habitats in the New Zealand alpine zone (Wilson 1976). Macroscopic examples include benthic crusts in pools and dark streaks where water percolates down rock surfaces.

Studies of New Zealand alpine algae have been few. 63 algal taxa present in 38 samples from a range of habitats in Mt Cook National Park have been identified, mostly to generic level, without the use of cultures (Wilson 1976). These samples were collected opportunistically and do not represent an intensive study of a single site. Similarly, algae causing coloured snow were identified to generic level in samples from 16 sites in Arthur's Pass and Mt Cook National Parks, using direct microscopic examination of living and preserved field specimens (Thomas and Broady 1997). Description of the flora of some alpine tarns (Nordstedt 1888, Croasdale and Flint 1972) and two tentative identifications of preserved field specimens of snow algae (Hardy 1966, Kol 1968a) constitute the only other published research on New Zealand alpine algae.

1.3. Unifying hypothesis of this investigation

A general hypothesis concerning distribution, dispersal and growth of algae in an alpine site is presented in Fig. 1.1. This can be stated as follows. A strong seasonal influence is exerted by changes in the extent of snowcover. Winter is characterised by

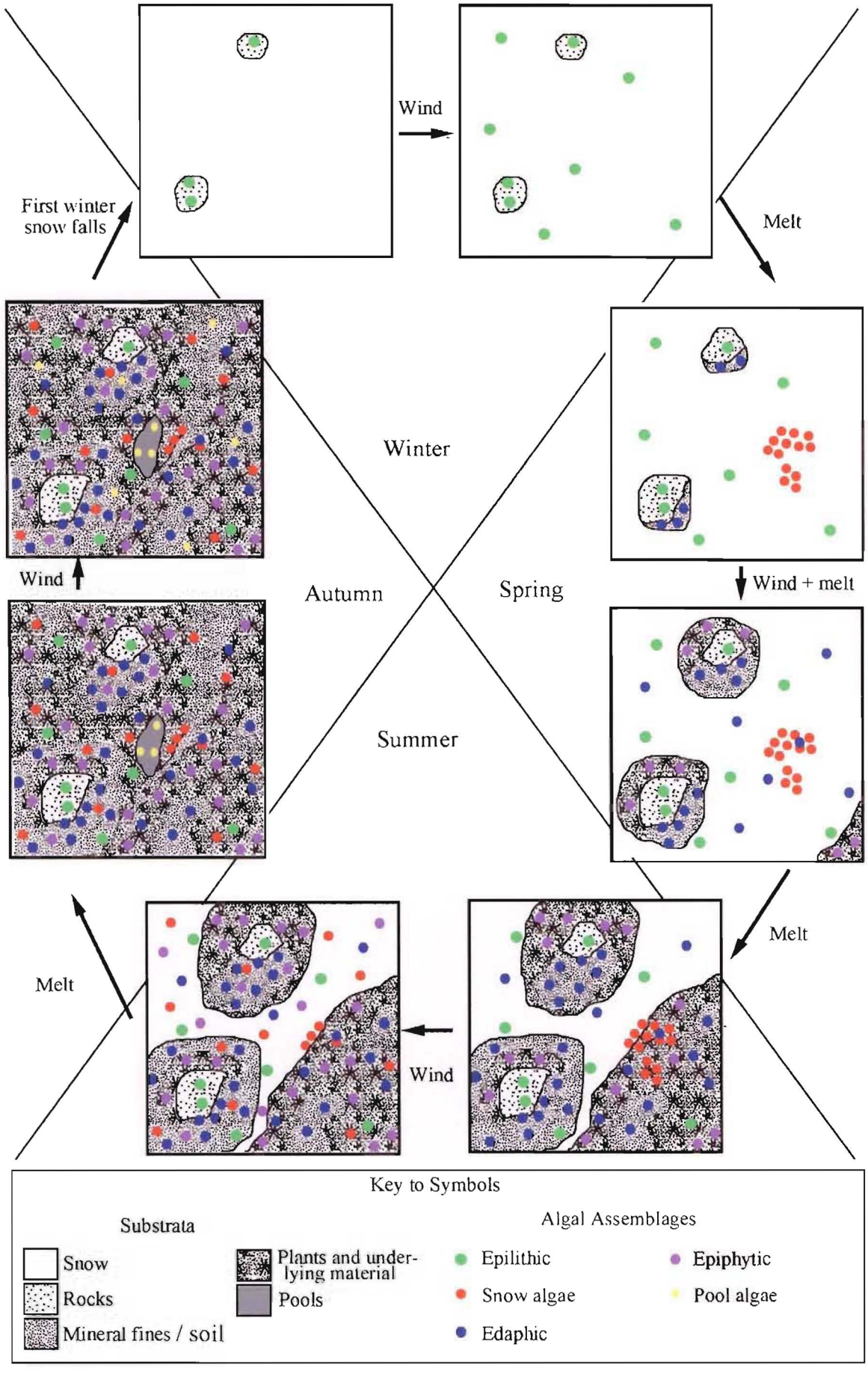


Fig. 1.1. Diagrammatic representation of unifying hypothesis of this investigation. See text for explanation.

extensive snowfields. Rocks (with whatever biota are attached to them) are the only other substratum exposed. Snow begins to melt in spring, slowly exposing underlying substrata and their associated algae, and creating favourable conditions for growth of snow algae, which require liquid water to be present in the snow (e.g. Fogg 1967, Hoham and Mullet 1977, Hoham and Mohn 1985, Mueller *et al.* 1998). Snow retreats further in summer and usually disappears before autumn, at which time all habitats on the site, including rocks, soils, plants, and pools, are exposed.

In the simplest scenario (Fig. 1.1), each habitat supports distinct algal assemblages, and propagules from them are dispersed elsewhere during summer. This makes two testable assumptions. Firstly, each type of habitat selects an assemblage of algae comprised of different species to those found in other habitats. Secondly, few or none of their propagules will be dispersed until the habitat in which they grow to significant abundance becomes exposed by snow retreat, either because they are numerically insignificant or do not survive over winter in habitats in which they are unable to grow.

Dispersal of snow algae is a special case, because they grow in snow but are not dispersed until the snow melts and their growth has ceased. However, melting is likely to deposit large numbers of snow algae onto underlying substrata following a bloom, prior to any dispersal. This deposition has been reported previously (e.g. Hoham 1971).

1.4. Testing the unifying hypothesis

In order to test this hypothesis, the present study has addressed the following questions.

- Where is a suitable site for the study of New Zealand alpine algae? Requirements for such a site are proximity to the laboratory, comparative ease of access, the presence of a variety of habitat types, and predictable occurrence of snow algae blooms. **Chapter 2: Study Site** describes the chosen location.
- The same species composition in all habitats on the mountain would disprove the hypothesis (Fig. 1.1). How are the different algae distributed between different habitats? Do any habitats support distinct assemblages? This question is examined in **Chapter 3: Distribution**.

In the case of snow algae, certain other questions are pertinent.

- Are snow algae at the site obligate (growing only in snow) or facultative (growing in snow as well as other habitats)? Are they a mixture of both? The hypothesis outlined above (Fig. 1.1) requires at least some to be obligate.
- The patchiness of alpine snow algae blooms is well documented, as is their recurrence at the same location every season (e.g. see Thomas 1972, Thomas and Broady 1997). What does this mean in terms of their growth and dispersal? Consider the previous question. If they are widely dispersed, but form blooms only in certain sites each year, some characteristic factor(s) of those sites must be amenable to bloom formation; i.e. not all snow is the same from the perspective of a snow alga. Therefore, what environmental factors might determine when snow algae can grow? **Chapter 4: Snow Ecology** is dedicated to this question.

The hypothesis above (Fig. 1.1) involves dispersal of algae between habitats.

- How are the algae dispersed? Are algae not growing on the site being dispersed there? Are all algae growing on the site to be found in the aerobiota at all times, or is there a seasonal effect? An example of the latter which would support the hypothesis (Fig. 1.1) would be a predominance of species characteristic of rock surfaces blown onto snow during spring.
- Are snow algae dispersed by wind? If so, when? Initiation of mass blooms of snow algae by wind-dispersed resting cysts from other habitats has never been reported. According to the hypothesis above (Fig. 1.1), their airborne dispersal should not occur until the snow in which the population is growing has melted. How far are they dispersed? Can they be detected in aerobiota in areas where there are no visible blooms? These questions form the basis of **Chapter 5: Dispersal**.

To attempt to answer all these questions, and to place the research in context with other studies, taxonomic investigation is required.

- Which algae occur in these alpine habitats? The answer to this question forms the basis of **Chapter 6: Taxonomy**.

CHAPTER 2.
STUDY SITE

2.1. Location

The study site is located in the alpine basins of Mt Philistine, Arthur's Pass National Park (Fig. 2.1). Mt Philistine is 1967 m high, located at approximately 171°31' E longitude, 42°53' S latitude. It is removed to the west of the Main Divide of the Southern Alps by one river valley. Arthur's Pass is approximately 150 km north-west of Christchurch, the largest city in the South Island of New Zealand.

2.2. Climate

Orographic rainfall and westerly to north-westerly winds dominate the climate of the National Park. The park spans the Main Divide of the Southern Alps for about 15 km on either side, so annual rainfall varies dramatically from one side to the other (Burrows 1974). Otira township to the west receives about 5 000 mm rain per year, Arthur's Pass village 4 km to the east about 4 000 mm, and Bealey, 10 km further east, about 1 500 mm. An exact figure is unavailable for Mt Philistine but it would be higher than Otira due to the higher altitude and prevalence of cloud even during fine weather. Most winter precipitation falls as snow. The wettest month on average at Arthur's Pass Village between 1916 and 1968 was October, with 444 mm of rain, and the driest was July, with 257 mm. However, considerable variation is possible between years. An estimated monthly rainfall chart for 1980 at Temple Basin, across the valley from Mt Philistine, is provided (Fig. 2.2).

A yearly temperature record is not available for Mt Philistine. However, the record of Burrows (1974) for Rough Creek Basin indicates that January is the warmest month in the Arthur's Pass alpine zone, and June to September the coldest months (Fig. 2.3). Snowcover at the site is strongly seasonal (Fig. 2.6a-f).

2.3. Geology and soils

The rocks of Mt Philistine are classified as cross-bedded, laminated, and homogeneous thick-bedded sandstone, with alternating sandstone and siltstone sequences. Thick bedded, locally strongly cross-bedded sandstone predominates of Otamitan-Oretian (Late Triassic) age. This is part of the Terebellina zone, in the Torlesse supergroup (Cave 1987). Where soils are present in the alpine and subalpine

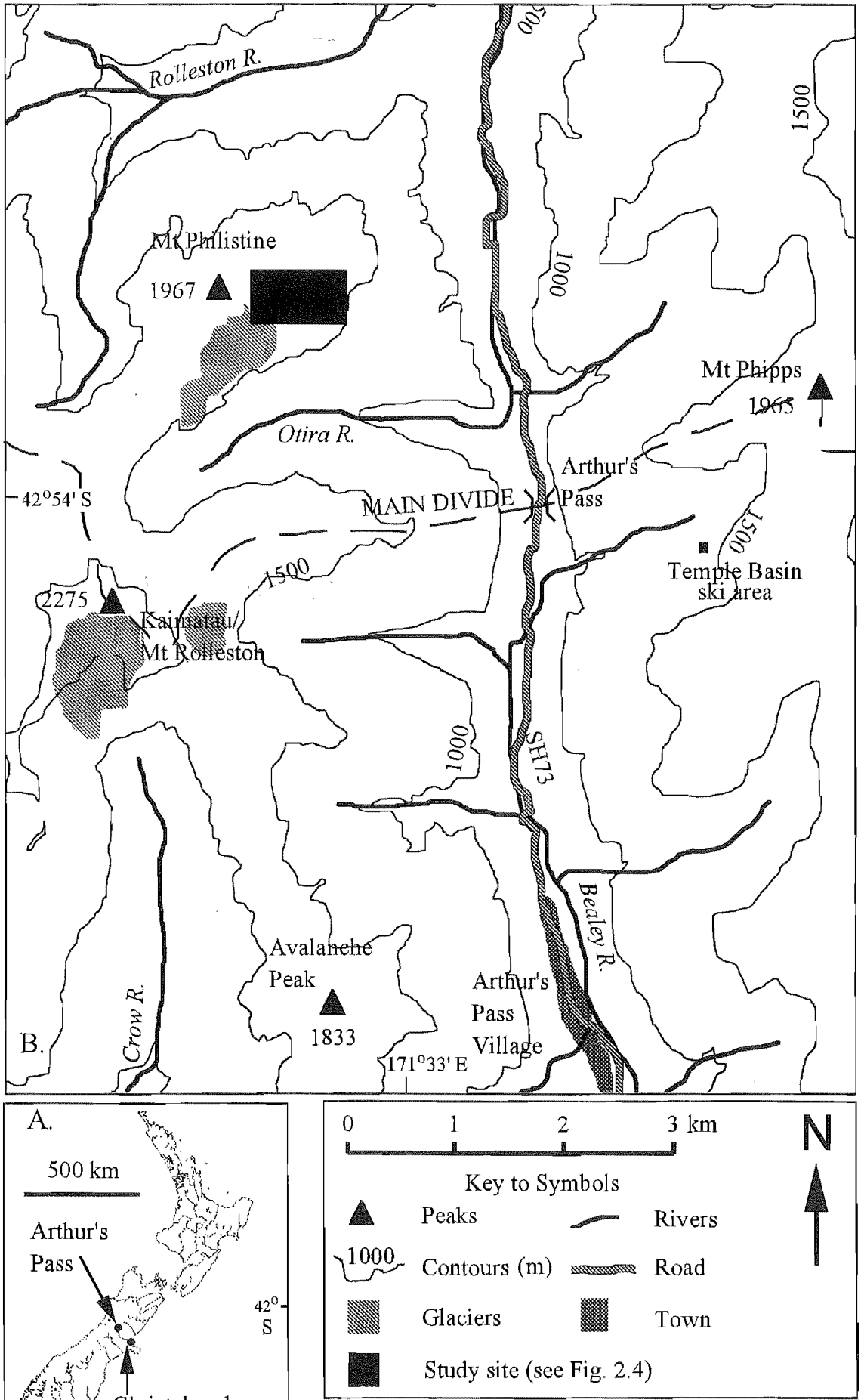


Fig. 2.1. Locality maps of study site. A, New Zealand and location of Christchurch and Arthur's Pass village. B, Location of study site in Arthur's Pass area. All altitudes in m a.s.l.

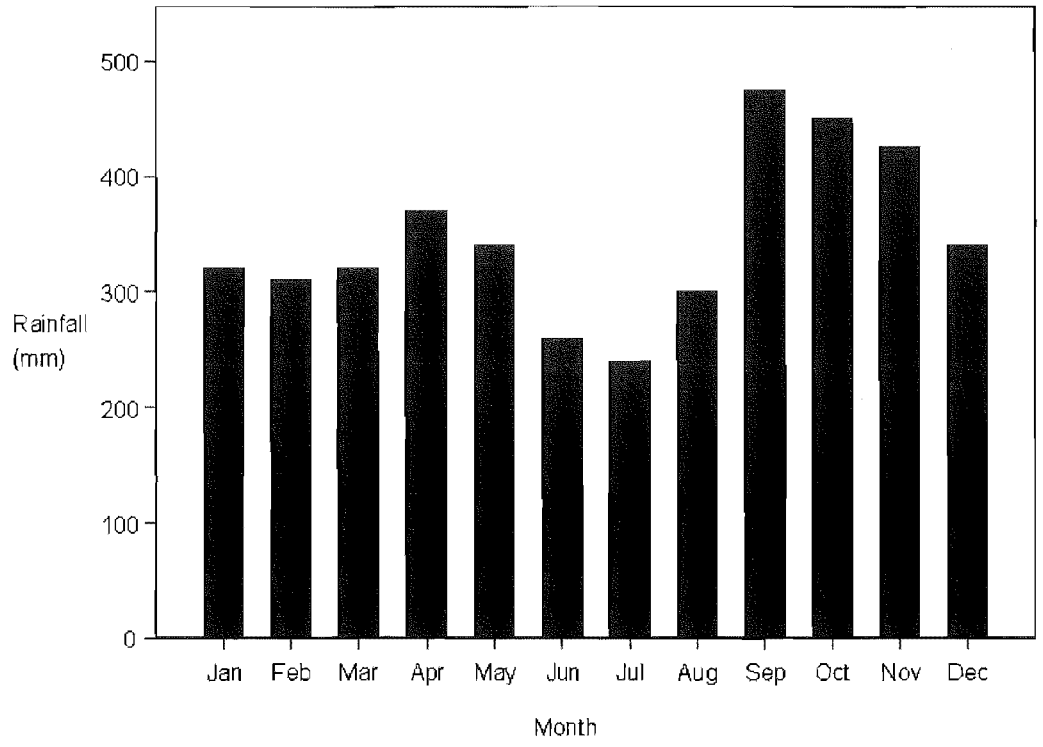


Fig. 2.2. Monthly rainfall at Temple Basin during 1980, estimated from Arthur's Pass data by adjustment for altitude difference (Palmer 1996).

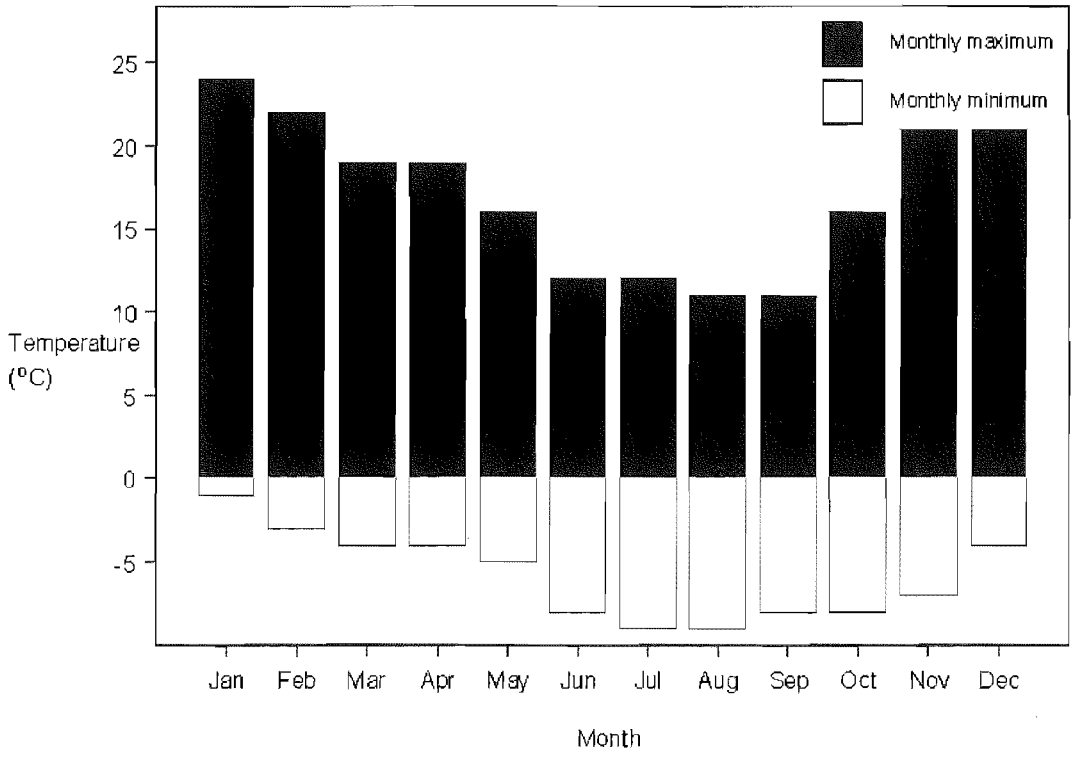


Fig. 2.3. Average maximum and minimum monthly temperatures at 1450 m, Rough Creek Basin above Arthur's Pass Village, 30 cm above ground surface, 1960-63 (data from Burrows 1974).

zones, they are thin and poorly developed (Dennis 1986), with a wide range of rock debris materials. Small areas of incipient soils in the form of organic / inorganic accumulations occur under the sparse vegetation (Cutler 1977).

Four major periods of glaciation occurred in the area during the last 500 000 years, the last major retreat occurring between 15 000 and 10 000 years ago. The remnant glaciers, including the Rolleston Glacier on Mt Philistine, have retreated substantially in the last 100 years (Burrows 1974).

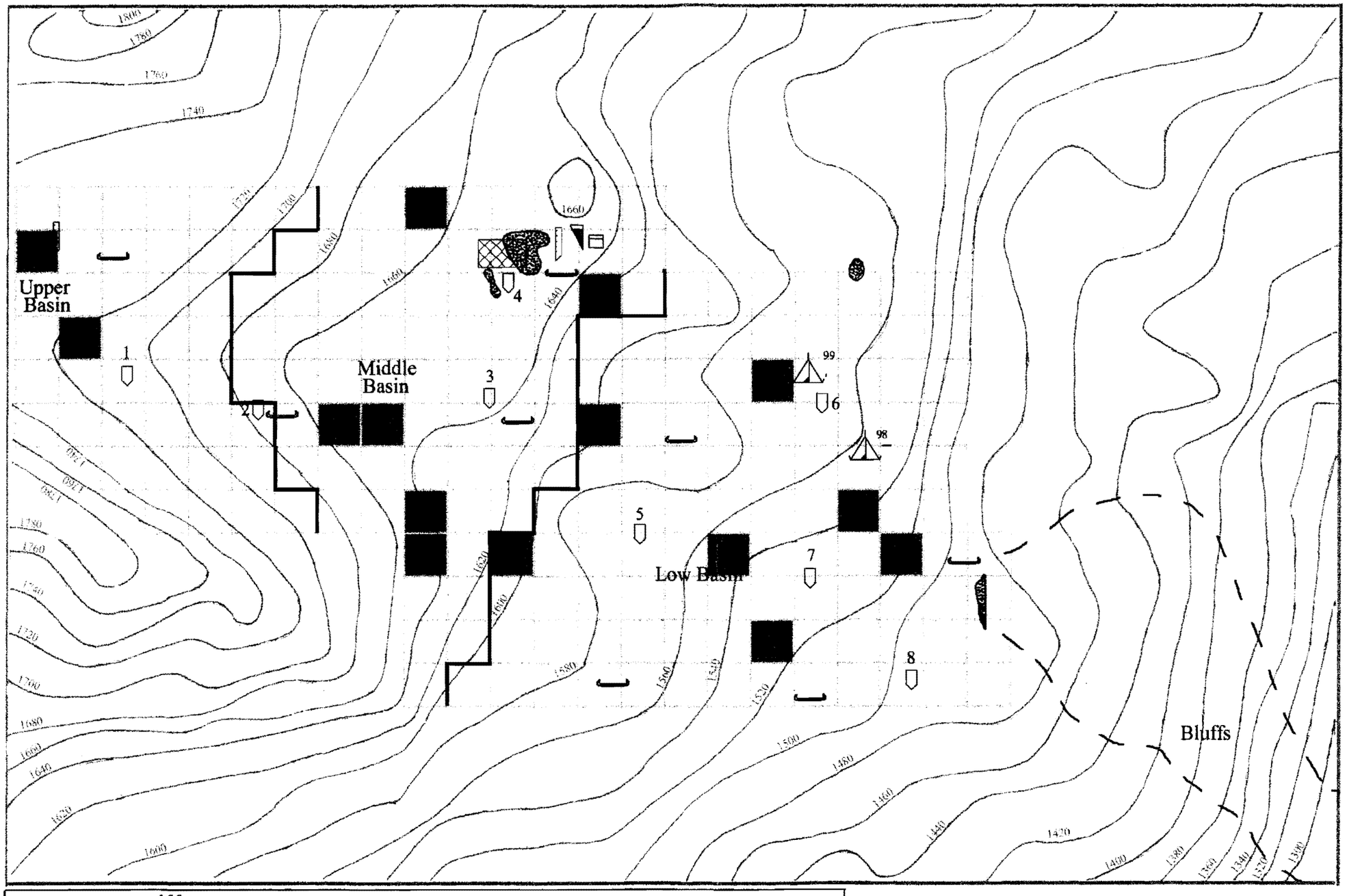
2.4. Flora and fauna

A large array of vascular plant species is present in alpine grassland communities, including several species of snowgrass (*Chionochloa* sp.), and alpine daisies (*Celmisia* sp.). *Andreaea* spp. are the most common mosses, occurring with a variety of lichens (Burrows 1974).

The treeline in Arthur's Pass National Park is approximately 1 200 m altitude in the east and 1 060 m in the west; however, about and just west of the Main Divide it is usually 800 m or lower. For this reason the definition of the "alpine" zone must be reasonably flexible. On Mt Philistine it was defined as higher than 1400 m a.s.l. according to the plant communities present (Burrows 1974). A band of subalpine scrub about 150 m wide extends above the treeline, giving rise to alpine herbfields and snowgrass above. The highest altitude populations of vascular plants reach about 1 600 m on Mt Philistine, although scattered specimens may be found higher (personal observations).

The treeline in North America, where much research on snow algae has been completed, is considerably higher relative to the snowline. For example, snow remains among *Pinus abicaulis* at 3 050 m in the Sierra Nevada, California, during spring (Thomas 1972).

Two native birds, the kea (*Nestor notabilis*, Fig. 2.6g) and the rock wren (*Xenicus gilviventris*) are found on Mt Philistine. The most commonly observed insect during summer is the alpine grasshopper (*Brachaspis colinus*). Hares (*Lepus europaeus*) and chamois (*Rupicapra rupicapra*), both introduced animals, venture as high as the study site in summer. For further information and references on flora and fauna of the area, refer to Burrows (1974).



100m

Vertical interval between contours = 20 m

N

Key to symbols

- 30 x 30 m squares defining study area
- Graduated snow stakes (snow depth)
- Rain gauge and light meter 1999
- Access routes
- 98 Campsite 1998
- 1998 snowfield ablation markers
- Frisbee aerobiota collectors 1999 (Ch. 5)
- 99 Campsite 1999
- Tarn snow algae study area (Ch. 4)
- Areas sampled for distribution analysis (Ch. 3)
- Tarns

Fig. 2.4. Map of study site showing low, middle and upper basins, and locations of recording and collecting apparatus. See Fig. 2.1 for site location.

2.5. Human history

The Arthur's Pass area was visited first by Māori, who often used Hurunui Saddle (Harper's Pass) to the north to cross the Southern Alps. Although what is now called Arthur's Pass was known to Māori, it had not been used in living memory at the time of its first crossing by Pākehā in 1864 (Dennis 1986, Logan 1990).

Arthur's Pass figured prominently in formation of a land link between Christchurch and the goldfields of the West Coast in 1866. The land link was of limited commercial use, however, before the completion of the Otira rail tunnel beneath the Pass in 1923 for transport of coal and timber to Christchurch. Many buildings in Arthur's Pass township on the east of the pass and Otira to the west date from this construction.

Areas to the south in the Waimakariri Basin began to be used for pastoralism in the 1860s, and this use continues. Mountaineering began with the first ascent of Mt Philistine in 1891, the peak named after one of the horses which transported the climbers from Christchurch. Research began prior to 1900 by such eminent botanists as Dr L. Cockayne (Dennis 1986). A research station is now maintained at Cass, just outside the park boundary to the south, by the University of Canterbury. The wilderness value of the area has long been recognised and the National Park was gazetted in 1929.

State Highway 73 over Arthur's Pass is now one of three main roads which cross the Southern Alps between the west and east coasts of the South Island. Arthur's Pass itself, at an altitude of 920 m, is almost immediately beneath Mt Philistine (Fig. 2.1). The National Park Headquarters, operated by the Department of Conservation, is located in Arthur's Pass village, which has a resident population of approximately 40 people (Dennis 1986). The 94 497 ha National Park is popular for tramping (hiking), mountaineering, and skiing in winter.

2.6. General description of the study site

The site (Fig. 2.4) ranges from 1480 m to 1760 m a.s.l., and is about 21 ha in area. It can be separated into low, middle and upper basins (Fig. 2.4, 2.5b). Alpine herbfield and tussock, interspersed by rock outcrops and some small tarns, typify the low basin (Fig. 2.5c). Vascular plants are much rarer in the middle basin and almost non-existent in the upper basin, the landscape consisting mainly of large boulders and

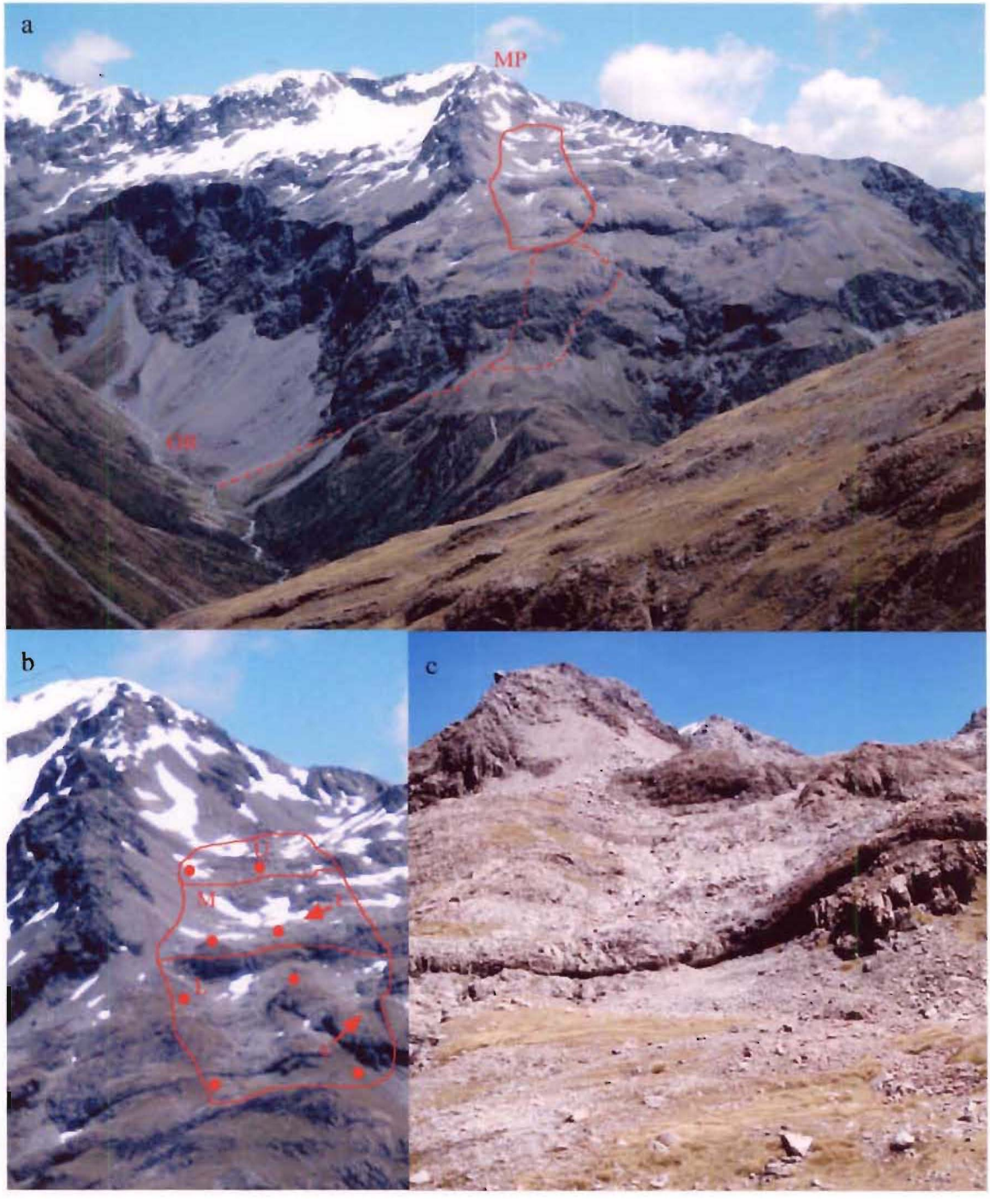


Fig. 2.5. Location of study site: a, Mt Philistine (MP) from Temple Basin, showing study area (solid line), access routes (dashed lines), and Otira River (OR); b, enlargement of study area covered by distribution (Chapter 3) and taxonomic (Chapter 6) surveys (U=upper, M=middle, L=low basins, c=campsite, t=tarn, study area of snow algae (see Chapter 4), solid circles=aerobiota collectors (see Chapter 5)); c, view from bottom of study site looking up towards Mt Philistine (patch of snow near summit). Photographs a, b taken December 1999; c taken January 2000.

Fig. 2.6. a, looking towards Mt Philistine from bottom of middle basin, 17 Nov 1998; b, same view on 28 Feb 1998; c, Mt Philistine from upper basin, early Sep 1999; d, similar view, 8 Nov 1999; e, tarn snow in middle basin, 1 Dec 1998; f, tarn on 28 Feb 1998 (circle surrounds figure for scale); g, Kea (*Nestor notabilis*), New Zealand's inquisitive and destructive alpine parrot.

snow (Fig. 2.6d). Small snow patches may remain throughout the year in the upper and middle basins; however, this would be very unusual in the low basin. The winter snowline is usually at about 1100-1200 m, with short-lived cover down to 900m or lower. Snow is usually absent below 1400m by 1 November.

A large tarn (approximately 500 m^2 surface area, Fig. 2.6e, f), which is snow-covered from winter to early summer, is present in the middle basin. This tarn snow develops blooms of red-pigmented algae every year (Table 2.1). Red snow in the middle basin was the reason for choosing this site as the study area. No tarns are present in the upper basin.

Access to the site (Fig. 2.5a) is steep; however, the site itself is a low-angled system of basins and spurs, among which travel is rapid and straightforward during fine weather. Thick cloud, a frequent occurrence in west of the Main Divide, hampers navigation, and the steep bluffs below the site mean that caution is required when travelling during these conditions.

Table 2.1. Sightings of visible snow algae blooms on Mt Philistine.

Date	Location	Dominant algae[1]
11 Mar 1997[2]	Middle basin below boulder scree	Chrysophyceae sp.1
19 Jan 1998[2]	Tarn surface snow, middle basin	*Chlainomonas kolii*
2 Feb 1998[2]	Tarn surface snow, middle basin	*Chlainomonas kolii*
Nov-Jan 1998-99	Tarn surface snow, middle basin	*Chlainomonas kolii*
Nov-Jan 1999-2000	Tarn surface snow, middle basin	*Chlainomonas kolii*, *Chromulina* cf. *elegans*

[1] Refer to Chapter 6 for authorities and descriptions.

[2] Sightings prior to start of detailed study on 1 November 1998.

CHAPTER 3.
DISTRIBUTION PATTERNS OF TERRESTRIAL AND SNOW ALGAE

3.1. Introduction

3.1.1. Distribution patterns of alpine terrestrial and snow algae

Distribution patterns of alpine algae in New Zealand have received little attention. The only previous study was made in Mt Cook National Park (Wilson 1976). Habitats sampled were tarns and pools, soil, exposed wood and rock surfaces, streams, and snow, from altitudes ranging from montane to alpine and nival zones. Most samples were taken during April, the time of least snowcover, and most algae were identified to genus level.

None of the snow algae recorded were found in other habitats, including pools at snow edges, and no algae from other habitats were found in snow. Desmids were mostly restricted to tarns and pools. The diatoms *Cymbella* and *Diatoma hiemale* var. *mesodon* (Ehrenberg) Grunow were confined to streams, whereas *Synedra* and *Tabellaria* were mostly found in tarns and pools. Four chrysophyceans were found, each occurring in only one sample. *Synura* and *Dinobryon* occurred in surface water of the same subalpine tarn. Cyanophytes occurred in all habitats except snow, but no individual taxa were widely distributed.

Of the other habitats sampled at Mt Cook, wood surfaces and soil supported the fewest species, and tarns, pools, and streams yielded the most. More species may have been detected, particularly from soil, if culture techniques had been used. Algae found in tarns and pools were generally not found in streams, and vice versa. Algae associated with mosses were not included in the study. Discussion of results was brief, the major focus of the work being the vascular plants of the national park. Other surveys of vegetation of New Zealand national parks (Travers 1972, Mark 1977, Atkinson 1982, Clarkson 1986) have not included the algal flora.

Distribution of snow algae in New Zealand was studied by Thomas and Broady (1997). In many cases colour of snow was the only information obtained; 41 of 45 such sightings were recorded in the Southern Alps during 1991-95, from Kahurangi National Park in the north to Mt Aspiring National Park in the south, with the remainder occurring in Tongariro National Park, North Island. Samples were examined from 16 sites in Arthur's Pass and Mt Cook National Parks, 15 of which contained species of *Chlamydomonas*. The genera *Koliella*, *Raphidonema*, *Cryocystis* and *Scotiella* were more rarely recorded. The latter two are now widely accepted as being life stages of species of *Chloromonas*. No cultures were made in this study.

Other studies including New Zealand alpine algae have been brief and taxonomic in focus. The flora of tarns on the Kelly Range (Nordstedt 1888) and Queenstown Hill (Croasdale and Flint 1972) have been described.

Studies of alpine algae elsewhere have focussed on snow, soil and epilithic communities. Distribution of alpine snow algae has been studied most extensively in Europe (e.g. Kol 1968b), although more significant taxonomic and ecological progress has been made in North American forested systems (e.g. Hoham 1975, Hoham and Mullet 1977, Hoham *et al.* 1979, 1983). Most studies of alpine soil and epilithic communities have been made in the European Alps, and studies of alpine terrestrial epiphytic algae are rare.

Ecology and distribution of snow algae is reviewed by Hoham (1980) and Hoham and Ling (1999), and relevant aspects are detailed in Chapter 4.

Culture studies on alpine soil algae from temperate regions have often been taxonomic in focus (e.g. Vischer 1945, Reisigl 1969, Desortova 1974, Vinatzer 1975). Soil algae from the Ötztaler Alps, Western Europe, were studied with a greater emphasis on distribution patterns (Reisigl 1964). Of six soil types examined, lime-rich mineral soils contained the highest proportions of the total species: 67% of cyanophytes, 56% of heterokontophytes, and 57% of chlorophytes. Only 2 diatom species were recorded.

Studies of distribution patterns of epilithic algae (reviewed by Nienow 1996) include several within the alpine zone, and have shown preferences of different species for different microenvironments. For example, communities growing on limestone outcrops in the Dinaric Alps have been grouped according to relative humidity of the sites (Golubić 1967). The flora included four species of *Gloeocapsa*, which dominated the driest sites, in the five most frequently encountered algae. An early study of distribution in epilithic alpine communities was undertaken in the Cevedale Mountains, Italy (Marchesoni 1939). Diatoms dominated the flora, and desmid species outnumbered other chlorophyte and cyanophyte species. This contrasts with epilithic limestone communities in the Maritime Alps, France (Fjerdingstad 1965), where cyanophytes were found to dominate, including the genera *Gloeocapsa*, *Calothrix*, *Chroococcus*, *Microcoleus*, *Myxosarcina*, and *Nostoc*. No diatoms were recorded, which supports the suggestion that they are not well-adapted to subaerial habitats (Nienow 1996). Communities of epilithic algae have been grouped according to rock type elsewhere in the European Alps (Jaag 1945), where 92 species were unique to silica rocks, 30 to lime dolomite, 15 to sandstone, and 28 were found on all rock types.

Effective use has also been made of ordination procedures to group such communities in Nant Porth Quarry and Cwm Idwal, Wales (Allen 1971), according to wetness, sun exposure, steepness, pH and type of rock.

3.1.2. Distribution patterns of polar terrestrial and snow algae

Many habitat features, such as climate, vegetation (mosses and lichens), and prevalence of mineral soils, are common to both polar and alpine environments. As a result, an overview of some important studies of the distribution patterns of algae in polar habitats is worthwhile.

Antarctica is of particular interest when considering algae of alpine New Zealand because of its relative proximity. Studies of the distribution patterns of Antarctic terrestrial algae are reviewed by Broady (1996).

Aerial and subaerial habitats on Signy Island, Antarctica, are dominated by cyanophytes (Broady 1979a). The aerial habitat contains fewer species (34, compared to 150 in the subaerial), and is a harsher environment for growth due to poor water retention and exposure to strong winds. Diatoms are the only group to be more species-rich in aerial habitats than in other habitats at this location. High species richness occurs in mineral fines and in soil beneath the grass *Deschampsia antarctica*, but a poor flora is associated with *Polytrichum – Chorisodontium* moss turves. These features were also found in a preliminary survey of the Antarctic Peninsula and South Georgia (Broady 1979b). However, in the continental sites there is a species-poor diatom flora (Broady 1979b, 1996).

In northern Victoria Land, continental Antarctica (Broady 1987b), epiliths are dominated by *Ulothrix* sp, *Melosira setosa*, and lichens, except when influenced by bird populations, where cyanophytes and *Prasiococcus calcarius* (Pet.) Vischer become dominant. Therefore, the nutrient status of different sites can profoundly influence these assemblages. Oscillatoriaceae are the most common group in soils, mosses, streams and ponds. Other common algae include chlorophytes and diatoms in soils influenced by penguins, *Nostoc* sp. and unicellular chlorophytes on mosses, and chlorophyte filaments in streams.

A variety of different pond types have been studied in ice-free areas of Ross Island (Broady 1989a). Pools most closely resembling those found on Mt Philistine, those classed as "typical" ponds, are dominated by oscillatorialean filaments. Green snow found in these areas was always close to the ocean and undergoing considerable

melting and fertilisation by penguins. Rapid flowing, steep streams contain either no algae or only epilithic growths, whereas reddish oscillatorialean felts are more common in relatively slow moving water. Oscillatoriaceae and *Nostoc* are common on poorly drained lithosols on exposed ground, but *Nostoc* is absent whenever sites are influenced by sea spray, and *Prasiola crispa* (Lightf.) Menegh. proliferates wherever nutrient enrichment occurs (Broady 1989a).

Gloeocapsa spp. dominate epilithic growths in Marie Byrd Land (Broady 1989b), sometimes in combination with *Stigonema* sp. Combinations of *Cyanothece aeruginosa*, *Stichococcus bacillaris*, and *Pseudococcomyxa simplex* are common in free-living associations with lichens, in mineral fines and as epiphytes on moss.

High species richness of algae in certain snowfields of Cierva Point, Antarctic Peninsula (Mataloni and Tesolin 1997), includes cyanophytes and diatoms, many of which are also common to mineral soils surrounding the site. It is likely that the presence of these organisms in snow is a result of wind or water-mediated transport. However, many species were present which are considered to be obligate snow algae, including *Chlamydomonas nivalis*, *Chloromonas bolyaiana* (Kol) Gerloff and *Chloromonas brevispina*, all of which were dominant at various sites.

A detailed survey of the Windmill Islands region has been completed, revealing 145 non-marine taxa. Twenty-four of these occur in snow, nearly half of which are obligate snow algae (Ling and Seppelt 2000). *Chloromonas rubroleosa*, an alga of red snow, is one of several algae common to the Mt Philistine study site (see Chapter 6: Taxonomy). The Windmill Islands study demonstrates the existence of facultative snow algae, which may grow in environments other than snow. *Raphidonema nivale* Lagerheim is an example of a snow alga which is also thought to grow in soil (Hoham 1973) and has been found in a polar stream (Fukushima 1963). Distinguishing between wind-blown algae, facultative snow algae and obligate snow algae in samples is potentially a major problem. Wind-dispersed algae from other habitats, which contaminate snow, and are not true snow algae, have been labelled "cryoxen" (Kol 1942). A classic example is *Stichococcus* (Fukushima 1963, Hoham 1971).

Arctic studies have followed a similar pattern to those in Antarctica. Early studies of soil and aerial algae of arctic deserts and tundra (reviewed by Novichkova-Ivanova 1972) found that stony substrata favoured chlorococcalean algae. Oscillatorialeans and unicellular xanthophytes dominated loam of polygonal arctic deserts, and fewer xanthophytes were present on mosses than elsewhere. These observations may be due to slight acidity favouring xanthophytes and colonial green

algae on the Yamal and Gudan Peninsulas, and Oscillatoriaceae dominating in alkaline conditions. Widespread crusts of *Nostoc commune* in Taimyr soils are thought to be due to the accumulation of carbonate on the surface. Few cyanophytes were recorded in Arctic tundra habitats.

Ordination procedures have not been employed to date in published results of Antarctic algae distribution studies. However, at least one example exists for Arctic tundra soil communities in the Kaffiöyra Plain, Spitsbergen (Oleksowicz and Luścińska 1992). Reciprocal averaging (correspondence analysis, Digby and Kempton 1987) and cluster analysis revealed that cyanophytes and diatoms grouped in separate areas according to wetness of habitat, but bryophytes were not useful for distinguishing these groups. Chlorophytes (mostly desmids) were scattered throughout habitats.

A recent distribution study of polar desert soil algae was made near Sverdrup Pass, Ellesmere Island (Elster *et al.* 1999). Granitic soils were richer in chlorophytes, whereas dolomitic soils were richer in cyanophytes. However, high diversity was not always associated with high biomass.

3.1.3. Techniques used in the investigation of distribution patterns of polar and alpine algae

Floristic surveys typically include some mention of the habitats from which each organism was described or isolated (e.g. Reisigl 1969, Desortova 1974, Vinatzer 1975, Plichta and Luścińska 1988). This provides the most basic information on distribution patterns. Some studies tabulate this information, making trends easier to detect, and give numbers of species in each division present in each habitat (e.g. Marchesoni 1939, Jaag 1945, Reisigl 1964, Broady 1979a).

Detection methods vary between studies. Those making use of culture techniques (e.g. Vinatzer 1975) typically detect many chlorophytes, whereas those using only direct microscopic examination (e.g. Plichta and Luścińska 1988) tend to find more cyanophytes and diatoms. Some studies examine only a subset of total habitats, which will not necessarily give a realistic idea of distribution patterns (see Broady 1996 for examples).

Ordination procedures, which allow perhaps the most effective visualisation of trends in results, have been applied in few cases (e.g. Allen 1971, Oleksowicz and Luścińska 1992). Allen (1971) stated that much information in the study of Marchesoni (1939) had been missed due to the absence of ordination.

Ideally, therefore, studies of the distribution of algae in newly examined areas should include all recognisable habitats, using both direct observation and culture techniques (Broady 1996), and the results should be subjected to an ordination procedure.

3.1.4. Aims

Distribution of alpine algae over a range of habitats in a single New Zealand site has never been intensively studied. The Mt Philistine algal flora has not been examined previously. The following are the basic questions of interest.

- Where do algae occur on the study site?
- Are snow algae present in habitats other than snow?
- Do algae from other habitats on the mountain also occur in snow?
- Are any patterns evident in the distribution of algae among different habitats?

3.2. Methods

3.2.1. Selection of sites for sampling

A map of the study site (Fig. 2.1.1) was divided into 30 m x 30 m squares, which were numbered and separated into upper (28 squares), middle (85 squares), and lower (97 squares) basins. A random number table was used to select squares for sampling, until two in the upper basin, seven in the middle, and eight in the lower had been chosen. Each selection is approximately the same proportion, i.e. one fifteenth, of the total available for each basin.

3.2.2. Sampling procedure

Sampling was carried out on 9 December 1999. The corners of each square on the ground were located as accurately as possible by comparing the map with geographical features. All recognisable habitats were sampled once in each selected square. Habitats recognised were rock surfaces (supporting epilithic lichens and algae), pools, mineral fines, snow, *Andreaea mutabilis* Hook.f. & Wils. (a dark brown moss),

organic soil lacking vegetation (hereafter referred to as "soil"), and leaf material at the base of herbaceous and prostrate shrubby vascular plants (*Anistome imbricata* (Hook.f.) Ckn, *Gentiana bellidifolia* Hook.f., *Chionochloa oreophila* (Petrie) Zotov, *Ranunculus sericophyllus* Hook.f., *Haastia sinclairii* Hook.f., *Ourisia* sp., and *Hebe tetrasticha* (Hook.f.) Ckn. & Allan). Each sample (approximately 1-2 g) was removed directly into a sterilised 9 ml polycarbonate test-tube with a screw-top lid by pushing the uncapped tube through the material to be sampled. Two replicate samples were collected in each case, one for direct microscopic examination and one for cultures. Samples were refrigerated overnight at Arthur's Pass and for a further two days in the laboratory before analysis.

3.2.3. Analysis of samples

Three different methods of examination, described below, were used for each sample. Algae were compared to drawings and photographs made from previous samples, and new records made whenever new morphotypes were encountered (see Chapter 6).

a. **Direct microscopic examination.** A small amount of distilled water was added to the sample and shaken thoroughly (except for melted snow samples which were already suspended). A portion was placed on a slide to make a slurry and a coverglass placed on top. Plant materials (when present) were included in slurries to detect algae attached to their surfaces. Slides were examined using an Olympus BX50 microscope at magnifications up to 1000x. The entire slide was examined and the algae present were recorded. Slides were made repeatedly and examined until two consecutive slides from the sample contained no more additional algae. Preparation of diatom frustules for examination was according to the method of Cane (1996).

b. **Moist plate enrichment cultures.** For each sample, a small portion was placed in a sterile Petri plate of 5.5 cm diameter and moistened with sterilised distilled water. A flame-sterilised and cooled coverglass was then placed on top using flamed forceps, and light pressure exerted on the surface to embed the undersurface of the coverglass in the substratum. Plastic wrap was used to seal plates and reduce evaporation. Plates were randomised and placed in an incubator under quantum flux of 22-36 μmol $m^{-2}s^{-1}$ at 14°C, and

rearranged every 2 days to reduce position effects. Coverglasses were examined after 12 days incubation and algae recorded as above.

c. **Agarised mineral salt cultures.** Petri plates of 5.5 cm diameter containing full strength 1.2% agarised BG-11 medium (Rippka *et al.* 1979) were used for cultures. Double strength agar was washed for 5 days after autoclave sterilisation, by soaking in sterile distilled water and replacing the water each day. Medium and agar were autoclaved separately, cooled to ~45°C, and recombined before pouring plates. Two replicate plates were inoculated with 200 µl of each suspension made in (a) above, which was spread over the medium surface with a flame-sterilised glass spreader, and incubated as in (b), blocked by replicate. After 3 weeks, each distinct colony type on each plate was examined microscopically and the organism identified where possible. Newly recorded organisms were isolated into unialgal cultures for detailed examination and identification.

3.2.4. Analysis of results

Means of species richness data between habitats were compared using paired t-Tests in the statistical computer package S-Plus 2000 (Mathsoft 1999). Presence/absence data for all samples were combined into one matrix and detrended correspondence analysis (DCA), detrending by segments, with rare species downweighted, was performed using the statistical computing package Canoco 4 (ter Braak and Šmilauer 1998).

3.2.5. Distribution changes during snowfield retreat

Deposition of algae onto substrata beneath melting snowfields was investigated by comparing species in snowfield edges and underlying substrata following retreat of the snow. Single samples were taken from the surface of eight snowfield edges (see Chapter 2, Fig. 2.4, 1998 snowfield ablation markers, for locations) and from newly exposed substrata within 30 cm of the edge. Where possible, substratum samples were collected which were still wet from snowmelt. Small plastic markers were used to monitor snowfield retreat (see section 4.2). Samples were taken on 28 November, 2, 17, and 25 December 1998 and 1 January 1999. They were examined directly on site using

a Wild M11 field microscope with a gas lamp as light source, according to the procedure above (3.2.3a).

3.3. Results

3.3.1. Habitats and their distribution on the study site

A variety of habitats potentially containing algae was sampled. Snow was not coloured by algal growth except on the surface of the large tarn, which was not chosen for sampling by the random selection procedure (however, this was the location of the detailed study of snow algae; see Chapter 4). Other snowfields (Fig. 3.3.1d) were typically located in sheltered hollows with a light covering of fine wind-deposited material.

Mineral fines (aggregations of angular stones, <1 cm in diameter, Fig. 3.3.1a) did not support any macroscopic vegetation. Organic soils, exposed or supporting vegetation, were rare, only two samples being taken.

Where mosses and vascular plants were present, the plant material was sampled rather than the substratum. The moss *Andreaea mutabilis* was common as a stunted form occupying fissures and small irregularities on boulder surfaces (Fig. 3.3.1c), or growing more profusely in sheltered or irrigated locations (Fig. 3.3.1e). The latter situation also favoured the growth of *Anistome imbricata*. Other vascular plants sampled, *Gentiana bellidifolia* (Fig. 3.3.1f), *Chionochloa oreophila* (Fig. 3.3.1d, f), *Hebe tetrasticha*, *Ranunculus sericophylla*, *Ourisia* sp., and *Haastia sinclairii*, were more common in sheltered hollows than on exposed slopes.

Small temporary pools, up to approximately 1 m diameter and 0.1 m deep (Fig. 3.3.1c), were contained by hollows in rocks. Boggy depressions in soil and amongst vegetation which are present after rain were dry at time of sampling, because there had been no rain for some days and drainage occurs rapidly.

Exposed rock surfaces supported epilithic lichens (Fig. 3.3.1b, f). Although rock surfaces in depressions developed algal crusts, these were often covered with water and were therefore included in the "pools" category above.

The range of habitats varied greatly in the three basins sampled (Table 3.3.1). *Andreaea* moss and lichens were the only macroscopic vegetation found in the upper basin. *Andreaea* moss in the upper basin grew in a more stunted form than at lower

Fig. 3.3.1. Some habitats containing alpine algae on Mt Philistine: a, mineral fine (arrow) in boulder field, upper basin; b, lichen (arrow) on rock surface in middle basin (plastic tube is approximately 5 cm wide); c, melt pool on boulder surface, middle basin (arrow indicates small growth of *Andreaea mutabilis*, scale = 10 cm); d, typical retreating snowfield and recently exposed *Chionochloa oreophila* (arrow), lower basin; e, profuse growth of *A. mutabilis* (arrow) in water chute, middle basin (arrowhead indicates pack for scale reference); f, lichen (arrowhead), *C. oreophila* and flowering *Gentiana bellidifolia* (arrow) in lower basin. Photographs a, c, e, f courtesy of Paul Broady.

Table 3.3.1. Distribution and numbers of habitat samples taken from Mt Philistine study site, 9 December 1999.

Habitat	Number of samples			
	Upper basin	Middle basin	Low basin	Total
Snow	2	3	0	5
Mineral fines	2	5	7	14
Soil	0	0	2	2
Pools	2	6	2	10
Rock surfaces[1]	1	5	20	26
Andreaea moss	2	5	8	15
Vascular plants	0	6	38	44
Total	9	30	77	116

[1] Sampled when visible growths (epilithic lichens and algae) were present.

altitudes and was confined to cracks and fissures in rocks. Snow, mineral fines and pools were more frequently encountered in the upper basin than lower down the mountain.

Vascular plants were sparse in the middle basin and much more common in the low basin (Table 3.3.1). Epilithic growths were encountered more frequently in the low basin and snow was absent.

3.3.1. Algal flora of particular habitats

Assemblages of algae varied between some habitats, and different algae were recorded at different frequencies with different methods of detection (Table 3.3.2). Species richness in samples varied from 1 to 24 species (Fig. 3.3.2). Total species richness of chlorophytes in each habitat was generally higher than other divisions (Fig. 3.3.3), although mean species richness of chlorophytes and cyanophytes per sample was not distinguishable in snow, soil, melt pools or *Andreaea* (Fig. 3.3.4). Results from each habitat type are presented below.

Snow. Total species richness in snow was lower than in all other habitats (Table 3.3.2, Fig. 3.3.3), although mean species richness per sample was not (Fig. 3.3.4). The cyanophytes present in snow samples were cf. *Gloeocapsa*, *Cyanothece aeruginosa*, *Stigonema* sp., and cf. *Ammatoidea* (Table 3.3.2), which were common in other habitats and blown onto snow by wind. There is no evidence that these organisms grew in the snow (see Chapter 4: Snow Ecology). The only chlorophytes present in every snow sample were *Stichococcus* cf. *bacillaris*, and red snow cysts covered with mineral

Table 3.3.2. Algae observed, ordered according to overall frequency of occurrence and indicating frequency of detection by each method of sample analysis and by all methods in each habitat category.

Algae[1]	% Frequency of occurrence										
		Detection methods[2]			Habitats[3]						
	T[2]	DM	EC	MC	SN	MF	SO	MP	RS	AM	VP
CYANOPHYTA											
cf. *Gloeocapsa*	69	63	32	0	100	57	50	70	44	93	77
Cyanothece aeruginosa	48	48	18	0	20	50	50	80	11	100	50
Fischerella sp.	42	41	9	0	100	29	50	50	19	60	45
cf. *Ammatoidea*	29	29	9	0	20	14	0	90	4	80	20
cf. *Chroococcus*	16	4	13	0	0	14	0	20	0	73	9
Hormoscilla	16	12	7	0	0	14	50	10	0	47	18
Phormidium cf. *retzii*	12	4	8	3	0	7	50	20	0	13	18
Pseudanabaena cf. *tenuis*	8	3	8	1	0	7	50	10	0	47	0
cf. *Myxosarcina*	8	4	1	3	0	14	50	30	4	20	0
Leptolyngbya sp.1	3	1	0	2	0	0	0	30	0	0	0
cf. *Leptolyngbya* sp.2	3	0	2	1	0	7	0	10	0	7	0
Nostoc paludosum	2	2	0	0	0	7	0	0	0	0	2
cf. *Microcoleus*	1	1	0	0	0	0	50	0	0	0	0
cf. *Phormidium* sp. 2	1	0	1	0	0	0	0	0	0	7	0
EUGLENOPHYTA											
Euglena cf. *pisciformis*	3	2	3	0	0	0	100	0	0	0	5
CHLOROPHYTA											
Myrmecia cf. *irregularis*	69	39	14	44	0	93	100	60	52	80	77
Chlorella cf. *homosphaera*	50	22	9	34	0	71	50	20	78	33	45
Stichococcus cf. *bacillaris*	36	3	3	34	100	71	50	20	7	20	43
Klebsormidium flaccidum	33	13	15	23	0	57	100	40	4	27	45
Pseudococcomyxa simplex	33	4	3	32	0	36	100	20	7	27	55
Coccomyxa gloeobotrydiformis var.	27	8	3	24	0	57	100	20	7	20	34
Elliptochloris cf. *reniformis*	25	4	3	19	0	29	50	30	15	13	34
Red snow cysts (possibly *Chlamydomonas* sp)	24	22	4	0	100	21	0	80	4	20	18
cf. *Oocystis minuta*	17	3	3	11	0	21	0	0	11	7	30
Mesotaenium macrococcum var. *macrococcum*	14	9	5	0	0	0	0	0	0	40	23
Mesotaenium chlamydosporum var. *chlamydosporum*	12	5	9	0	0	14	0	20	4	27	11
Cylindrocystis brebissonii var. *minor*	10	7	6	0	0	7	100	10	0	20	11
Cylindrocystis crassa cf. var. *elliptica*	10	3	9	0	0	0	50	10	0	33	11
Chlorococcum tatrense	9	4	5	1	0	14	50	10	7	0	11
Chlorella cf. *minutissima*	9	0	5	6	0	21	0	20	7	13	5
Microthamnion strictissimum	8	0	3	7	0	43	0	0	4	0	7
Cosmarium decedens var. *decedens*	8	4	5	0	0	7	50	0	0	13	14
Klebsormidium elegans	7	2	0	5	20	7	0	10	0	13	7

cont.

Table 3.3.2. continued from previous page.

Algae[1]	% Frequency of occurrence										
		Detection methods[2]			Habitats[3]						
	T[2]	DM	EC	MC	SN	MF	SO	MP	RS	AM	VP
cf. *Mesotaenium*	7	4	4	0	0	7	0	10	0	33	2
Trochisciopsis cf. *tetraspora*	6	2	5	0	0	21	50	10	0	7	2
Chlamydomonas cf. *noctigama*	6	0	0	6	0	7	50	0	0	7	9
Myrmecia cf. *biatorellae*	6	0	0	6	0	0	0	0	4	7	11
Scotiellopsis terrestris	5	3	2	1	0	0	0	0	4	0	11
Chlamydomonas cf. *moewusii*	5	1	4	1	0	7	50	10	0	0	7
Stichococcus cf. *mirabilis*	4	1	1	3	0	14	50	0	0	7	2
Chlamydomonas cf. *culleus*	4	1	3	2	0	7	50	10	0	7	2
Coccothrix cf. *chlorolobata*	3	0	0	3	0	7	0	0	11	0	0
cf. *Chloromonas rosae* var. *polychloris*	3	0	3	0	0	0	0	0	0	0	7
Raphidonema nivale	3	0	0	3	60	0	0	0	0	0	0
Muriellopsis cf. *sphaerica*	3	0	2	1	0	7	0	0	0	0	5
Gloeocystis papuana	2	2	0	1	0	0	50	0	0	0	2
cf. *Pseudochlorella*	2	0	0	2	0	0	0	0	0	0	5
Chloromonas snow sp. 3	1	1	0	0	0	0	0	10	0	0	0
Zygnemataceae sp. 1	1	1	0	0	0	7	0	0	0	0	0
Chlainomonas kolii	1	1	0	0	20	0	0	0	0	0	0
HETEROKONTOPHYTA											
cf. *Achnanthes*	3	2	2	0	0	0	50	0	0	0	7
Xanthophyceae sp 1	3	3	2	0	0	0	0	10	0	0	5
Stauroneis cf. *prominula*	1	1	0	0	0	0	50	0	0	0	0
Total species richness	53	42	39	28	9	36	28	31	21	33	41
Number of samples (n)	116	116	116	116	5	14	2	10	26	15	44

[1] For authorities and taxonomic information, refer to Chapter 6.
[2] DM=direct microscopic examination, EC=enrichment culture, MC=mineral salts culture, T=total of all methods.
[3] SN=snow, MF=mineral fines, SO=soil, MP=melt pools, RS=rock surfaces, AM=*Andreaea* moss, VP=vascular plants.

particles. Other snow algae present in these samples were *Raphidonema nivale* and *Chlainomonas kolii*, in 60 and 20% of samples respectively.

Mineral fines. On average, more chlorophyte species were found in mineral fines than species of other divisions (Fig. 3.3.4). In total, 25 chlorophyte species, 11 cyanophytes, and no heterokontophytes were recorded. The total species richness of 36 was higher than all other habitats except vascular plants (Table 3.3.2). *Myrmecia* cf. *irregularis* was present in 93% of samples.

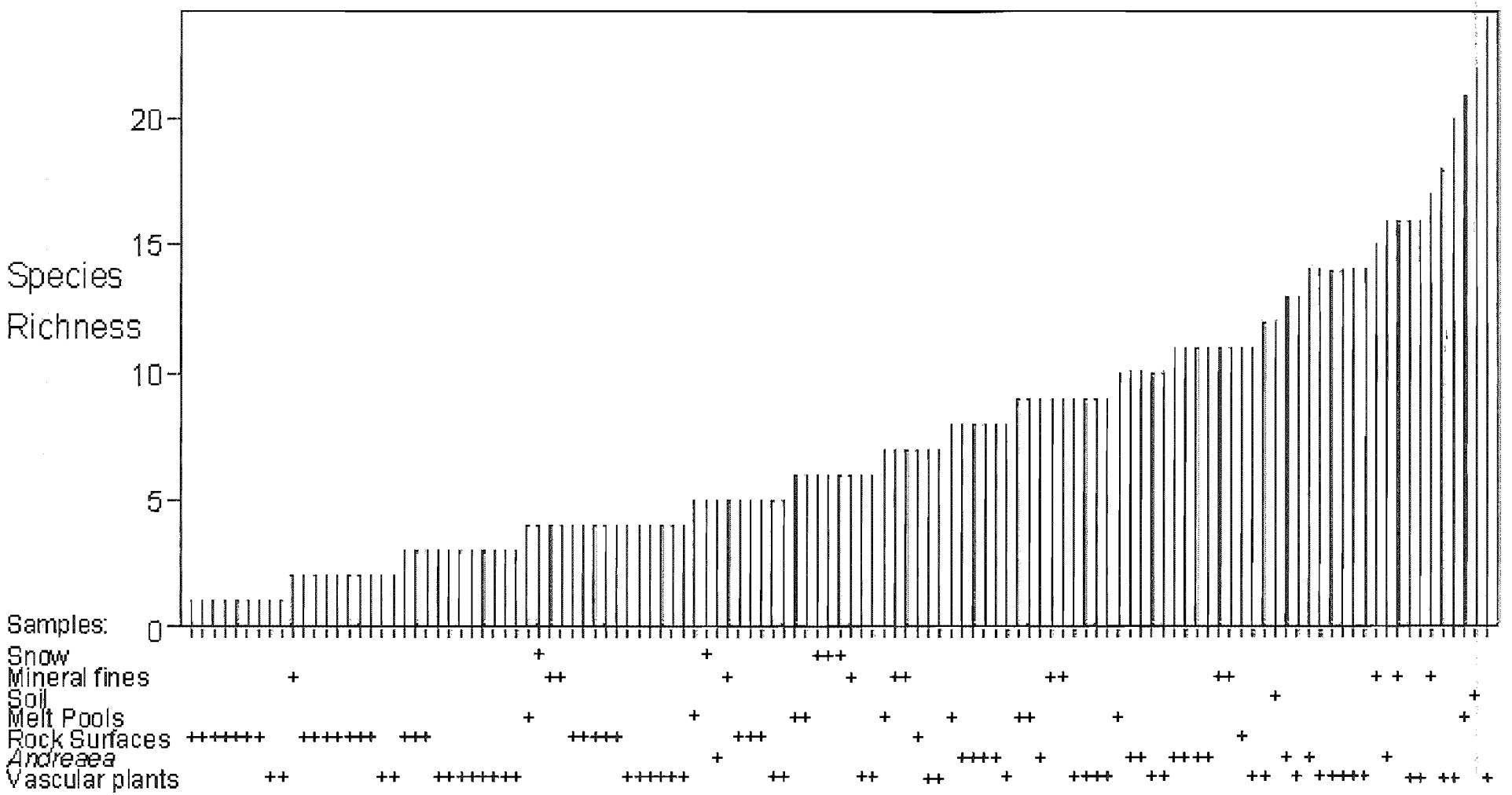


Fig. 3.3.2. Species richness in all samples taken, 9 December 1999, in ascending order. Habitat from which each sample was taken is indicated below each bar.

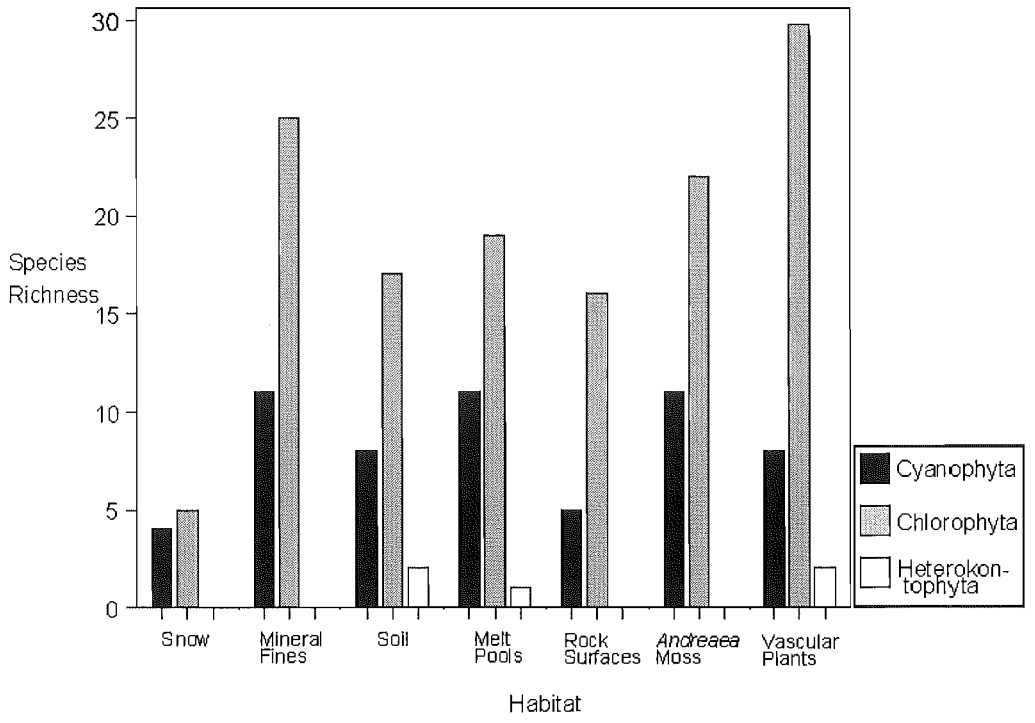


Fig. 3.3.3. Total species richness of different divisions of algae in each habitat type. Euglenophyta, represented by one rare species (see Table 3.3.2), is omitted.

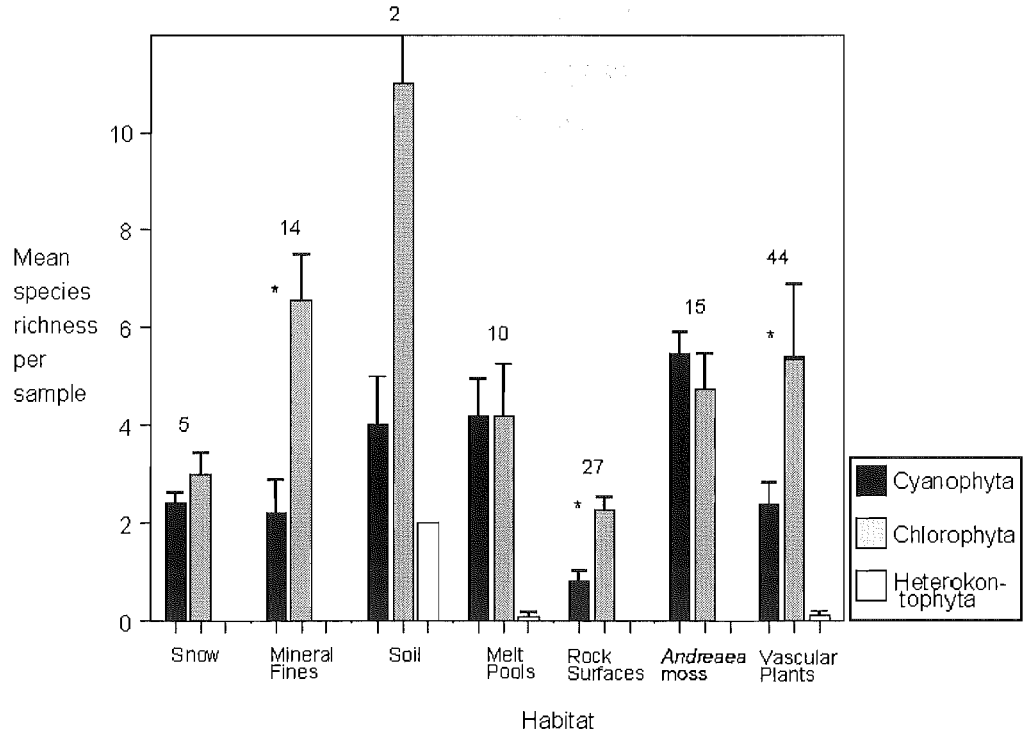


Fig. 3.3.4. Mean species richness per sample of each division in each habitat type. Data are means of n samples ±1SE. Habitats in which species richness of Chlorophyta is significantly greater than that of other divisions (paired t-Tests, $P<0.05$) are indicated by asterisks.

Soils. Although a rare habitat, bare organic soils supported 26 species, comprised of 7 cyanophytes, 17 chlorophytes and 2 heterokontophytes (Fig. 3.3.3), all found in two samples. The rarely encountered *Euglena* cf. *pisciformis* was found in both samples (Table 3.3.2).

Melt pools. 32 species were found in melt pools (Table 3.3.2). Mean numbers of chlorophyte and cyanophyte species in each sample were very similar (Fig. 3.3.4), although in total, more chlorophytes were found than cyanophytes (Fig. 3.3.3). Most melt pool samples had an intermediate level of species richness compared to other habitats (Fig. 3.3.2). Cf. *Ammatoidea* appeared to favour this habitat and was also the most common alga, occurring in 90% of samples (Table 3.3.2).

Rock surfaces. In general, samples from this habitat contained the fewest species (Fig. 3.3.2), most of which were chlorophytes (Fig. 3.3.4). A relatively high total species richness (Fig. 3.3.3) was recorded due to one exceptional sample (Fig. 3.3.2). *Chlorella* cf. *homosphaera* was the most common alga, occurring in 78% of samples. Species composition otherwise was quite variable, with the second most common, *Myrmecia* cf. *irregularis*, being present in only 52% of samples (Table 3.3.2).

***Andreaea* moss.** Most samples supported a relatively intermediate species richness (Fig. 3.3.2). Although more total species of chlorophytes than cyanophytes were recorded (Fig. 3.3.3), the mean number of species recorded from these divisions per sample were very similar (Fig. 3.3.4). Cf. *Gloeocapsa*, cf. *Ammatoidea*, and *Cyanothece aeruginosa* were especially common cyanophytes (all present in more than 90% of samples). The most common chlorophyte was *Myrmecia* cf. *irregularis* (80% of samples), no other chlorophytes being recorded in more than 40% (Table 3.3.2).

Vascular plants. Angiosperm surfaces yielded the greatest total species richness of all habitat types (Table 3.3.2), most of which were chlorophytes (Fig. 3.3.3). However, individual samples varied from very low species richness to very high (Fig. 3.3.2). Only two algae, cf. *Gloeocapsa* and *Myrmecia* cf. *irregularis*, were present in more than 70% of samples and no others were present in more than 50% (Table 3.3.2).

3.3.3. Comparison of the different methods used for detection of algae

Direct microscopic examination and enrichment cultures detected similar numbers of species (Fig. 3.3.5). However, fewer cyanophyte and no heterokontophyte species were recorded using mineral salt cultures. The only cyanophytes recorded using all three detection methods were *Phormidium* cf. *retzii*, *Pseudanabaena* cf. *tenuis*, and cf. *Myxosarcina* (Table 3.3.2). None of the six most common cyanophytes (present in more than 16% of all samples) appeared in mineral salts cultures.

By contrast, the seven most commonly recorded chlorophytes (occurring in more than 25% of all samples) were all found most frequently using mineral salts cultures, although all these organisms were recorded using all three methods (Table 3.3.2).

3.3.4. Grouping of habitats according to species composition

Detrended Correspondence Analysis (DCA) on presence/absence data from all sites indicates that many habitats have similar species assemblages (Fig. 3.3.6). Some habitat types grouped separately to others, however. Snow samples were grouped separately from all other habitats except some from pools and one from a vascular plant (Fig. 3.3.6, 3.3.7), and had a consistent assemblage of species. Species composition of *Andreaea* moss was distinct from that of rock surfaces (Fig. 3.3.7). Rock surfaces had the most variable species assemblages, with dispersion across more than 70% of Axis 1 and 80% of Axis 2, and contained fewer species than most other habitats (section 3.3.2).

Most samples of mineral fines grouped apart from pools (Fig. 3.3.8). Too few samples of bare soil were taken for sensible comment regarding their species assemblages to be made.

Algal assemblages on lower leaves of vascular plants differed little amongst species of plants (Fig. 3.3.9), but did group distinctly from *Andreaea* moss samples (compare Fig. 3.3.7 and 3.3.8).

3.3.5. Grouping of species according to habitat preferences

The most common algae on Mt Philistine, *Cyanothece aeruginosa*, *Fischerella* sp., cf. *Gloeocapsa*, and *Myrmecia* cf. *irregularis*, group in the central area of the ordination diagram (Fig. 3.3.10). Cf. *Myxosarcina*, *Nostoc paludosum*, cf. *Ammatoidea*,

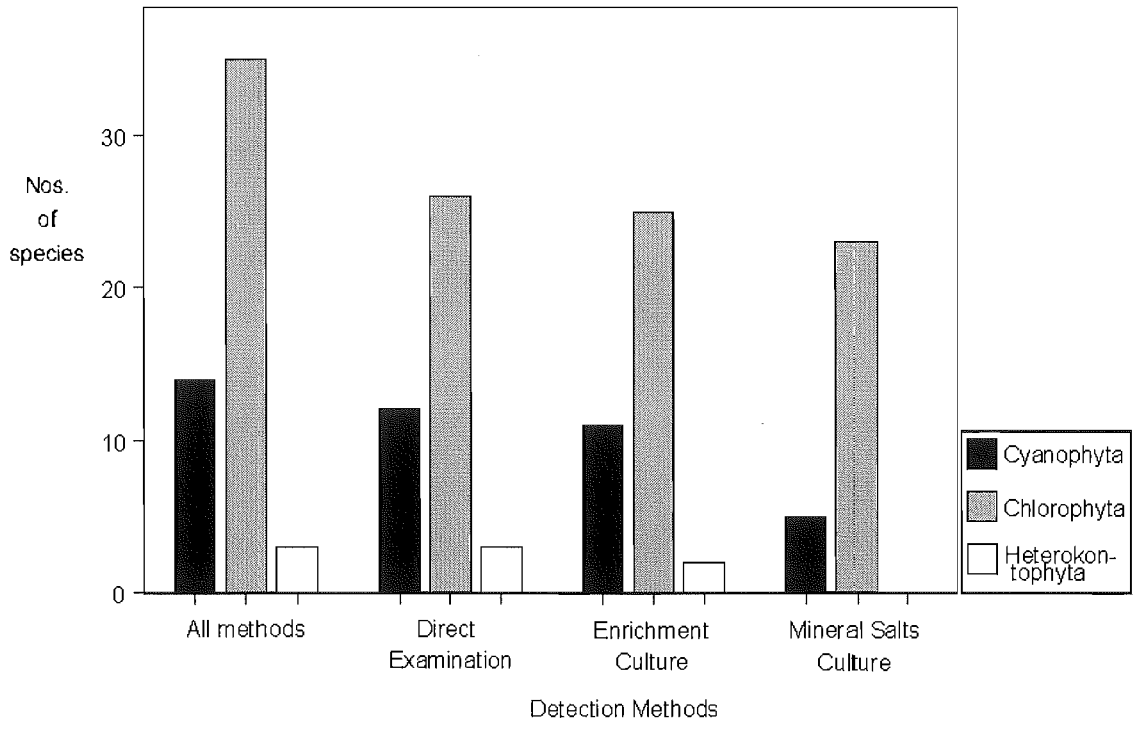


Fig. 3.3.5. Numbers of species of algae in divisions Cyanophyta, Chlorophyta and Heterokontophyta recorded using different detection methods.

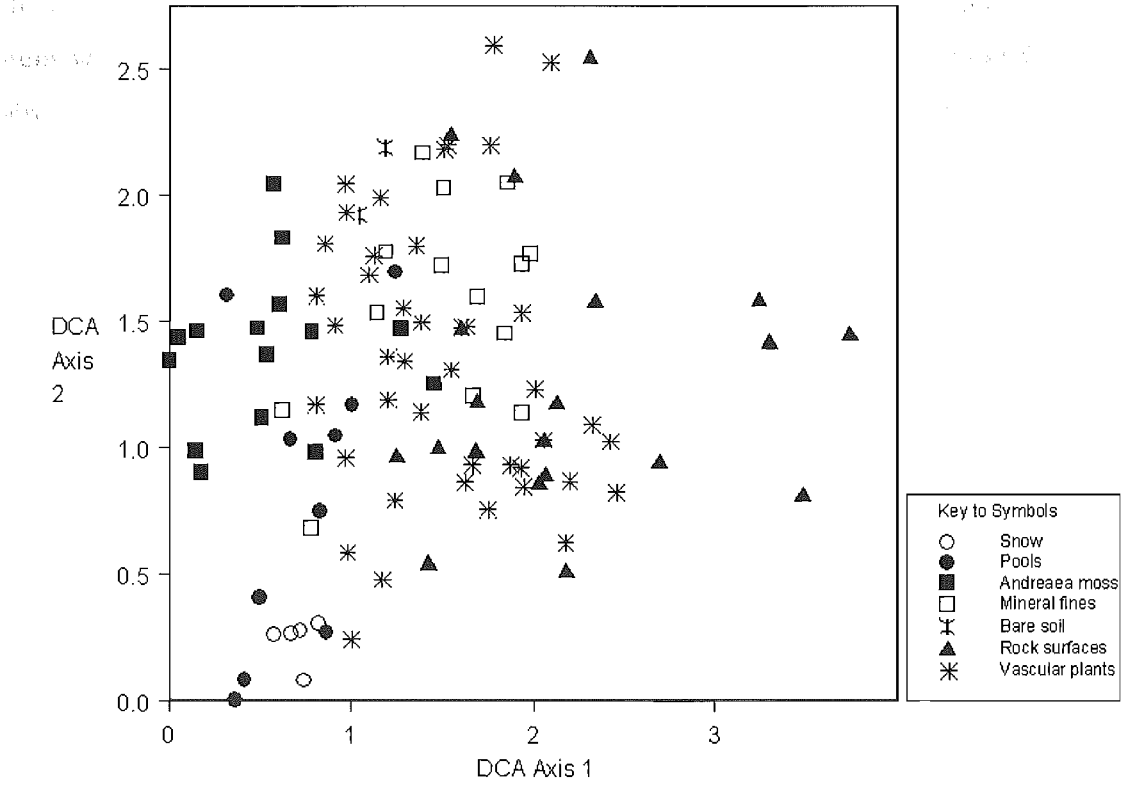


Fig. 3.3.6. DCA results from presence/absence data, grouping all habitats according to assmeblages of algal species on 9 December 1999 on the first two ordination axes. Cumulative variation explained is 9.4% for Axis 1, 16.2% for Axis 2. See Fig. 3.3.7 – 3.3.9 for clarified presentation.

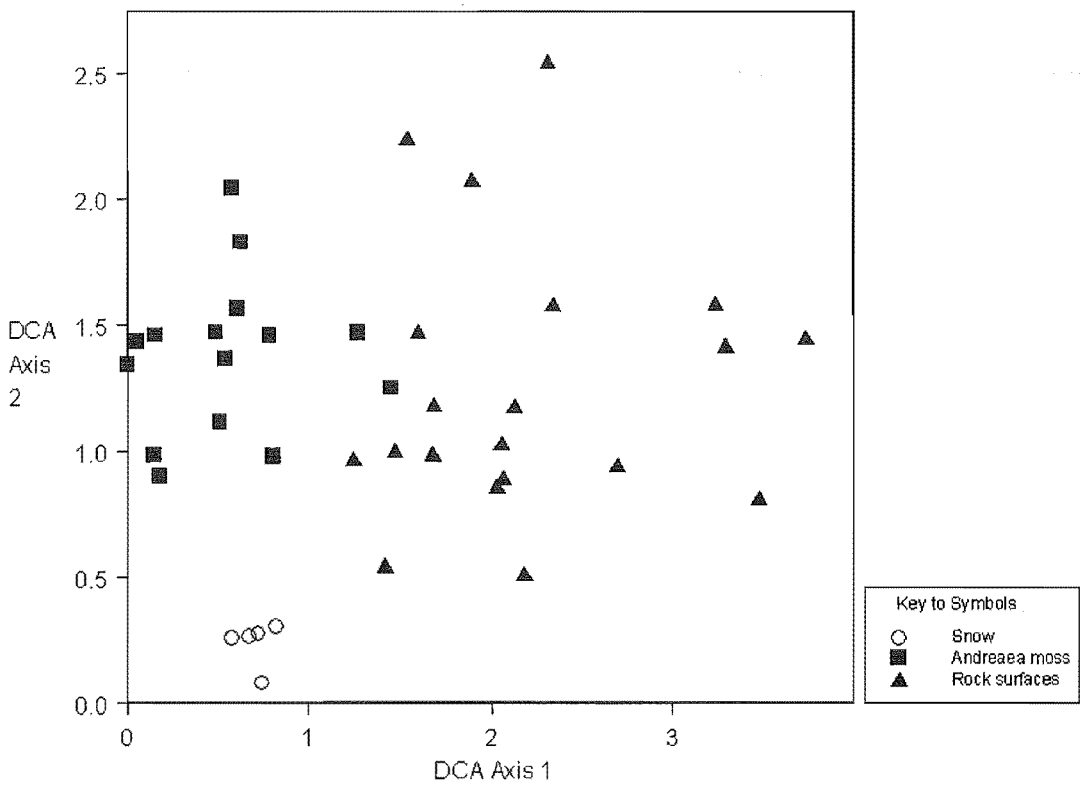


Fig. 3.3.7. DCA results from presence/absence data grouping snow, *Andreaea* moss, and rock surfaces according to their species assemblages, 9 December 1999.

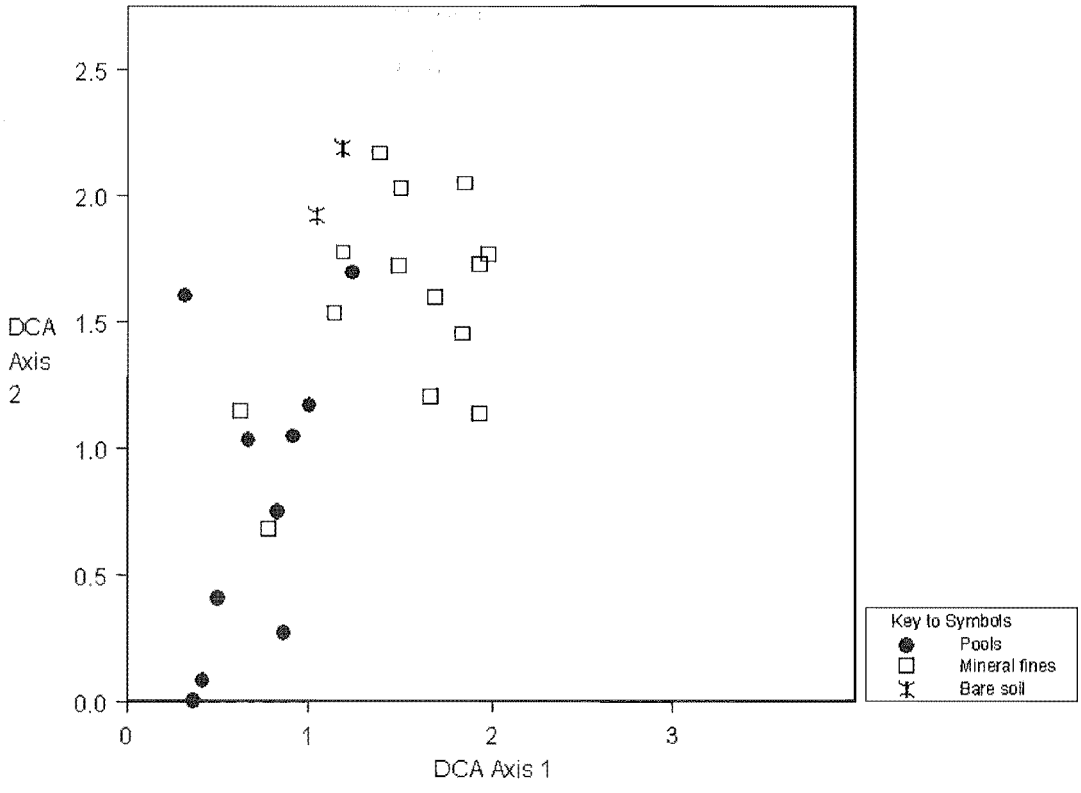


Fig. 3.3.8. DCA results from presence/absence data grouping pools, mineral fines, and soil according to their species assemblages, 9 December 1999.

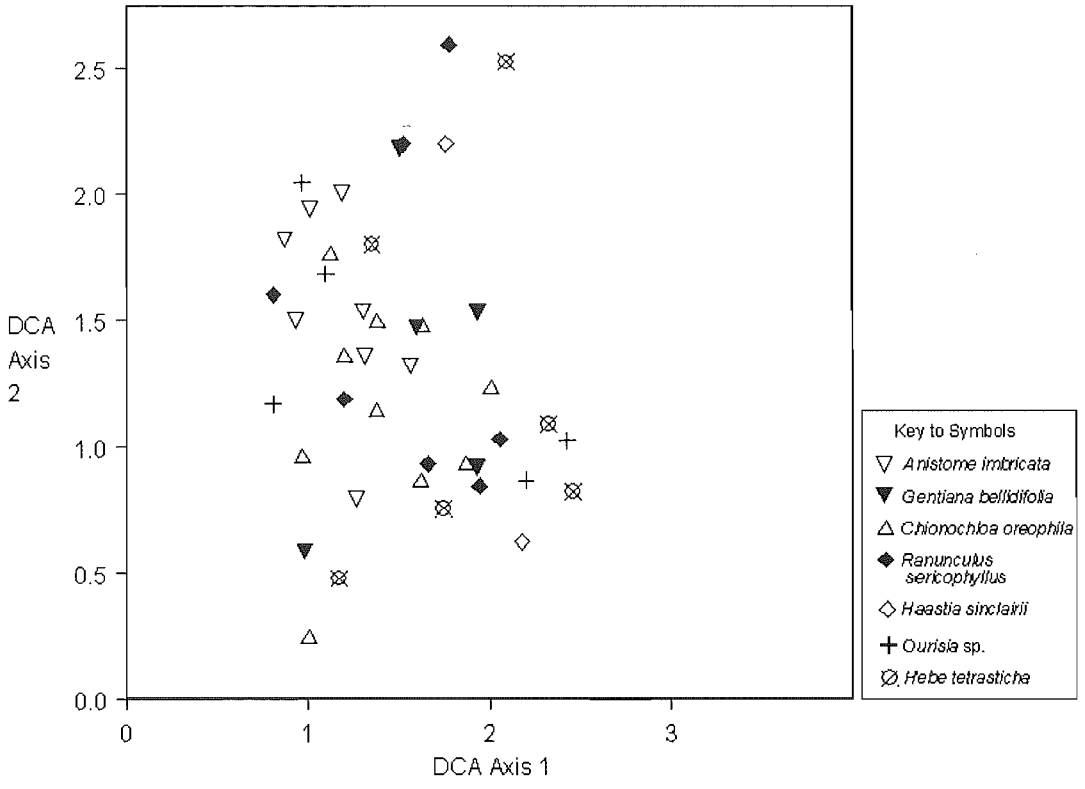


Fig. 3.3.9. DCA results from presence/absence data grouping different genera of vascular plants according to their species assemblages, 9 December 1999.

Leptolyngbya sp.1, cf. *Oocystis minuta, Klebsormidium elegans*, and red snow cysts, which occur less frequently but are also widely distributed among different habitats (Table 3.3.2), group in the same area.

Trochisciopsis cf. *tetraspora*, cf. *Zygnema*, *Chlamydomonas* cf. *moewusii*, and the desmids group closely (Fig. 3.3.10). These algae were linked by their almost total absence from rock surface samples (a large part of the data set), and were more commonly found associated with vascular plants than in *Andreaea* moss.

Species of the same genus which are common are the desmids *Cylindrocystis brebissonii* var. *minor* and *C. crassa* var. *elliptica*, and *Mesotaenium chlamydosporum* var. *chlamydosporum* and *M. macrococcum* var. *macrococcum*. These are grouped closely by the ordination. Species of the same genus, one or both of which are rare (occurring in less than 10% of all samples), do not group closely. This is the case for *Klebsormidium flaccidum* and *K. elegans*, *Leptolyngbya* sp.1 and cf. *Leptolyngbya* sp.2, *Chlorella* cf. *minutissima* and *C.* cf. *homosphaera*, *Stichococcus bacillaris* and *S. mirabilis*, and *Myrmecia* cf. *irregularis* and *M.* cf. *biatorellae*.

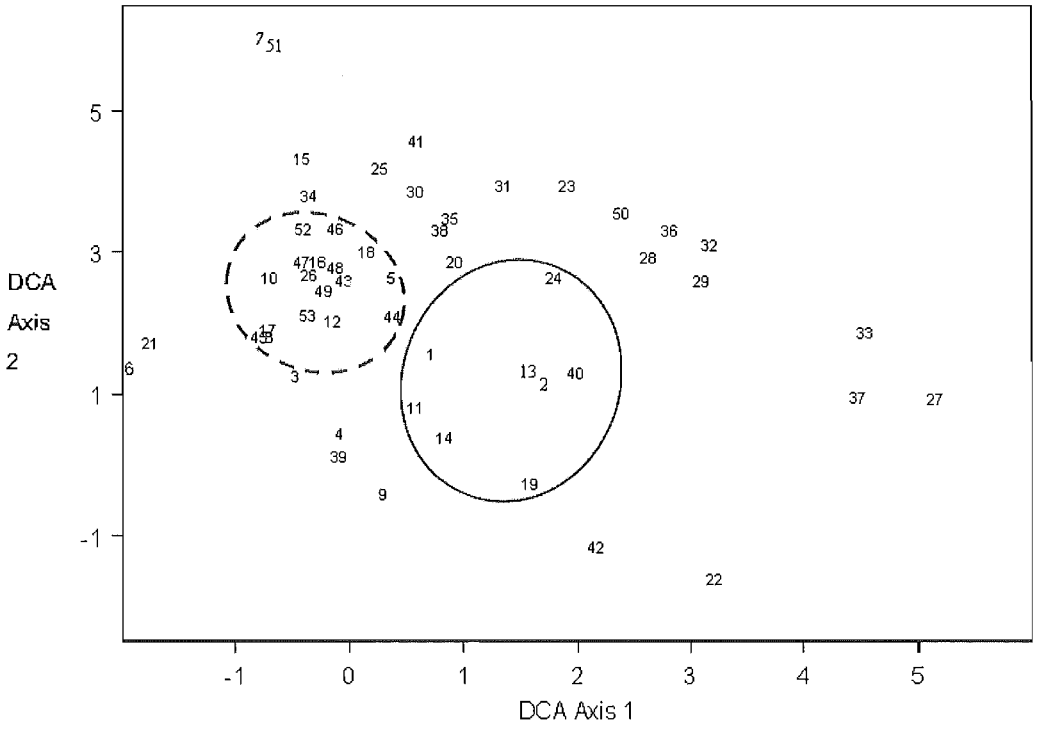


Fig. 3.3.10. DCA results from presence/absence data, grouping species according to habitats in which they occur. Dashed ring includes desmids, solid ring includes the most common species. Key to species numbers is presented below (for authorities and taxonomic information, refer to Chapter 6). Order of species corresponds to that in Chapter 6.

Cyanophyta

1 *Cyanothece aeruginosa*
2 cf. *Gloeocapsa*
3 *Chroococcus* sp.
4 cf. *Myxosarcina*
5 *Phormidium* cf. *retzii*
6 cf. *Phormidium* sp. 2
7 cf. *Microcoleus*
8 *Pseudanabaena* cf. *tenuis*
9 *Leptolyngbya* sp.1
10 cf. *Leptolyngbya* sp.2
11 cf. *Ammatoidea*
12 *Hormoscilla* sp.
13 *Nostoc paludosum*
14 *Fischerella* sp.
15 *Euglena* cf. *pisciformis*

Chlorophyta

16 *Chlamydomonas* cf. *moewusii*
17 *Chlamydomonas* cf. *culleus*
18 *Chlamydomonas noctigama*
19 Red snow cysts (possibly *Chlamydomonas*)
20 cf. *Chloromonas rosae* var. *polychloris*
21 *Chloromonas* sp 2
22 *Chlainomonas kolii*
23 *Chlorococcum tatrense*
24 *Myrmecia* cf. *irregularis*
25 *Myrmecia* cf. *biatorellae*
26 *Trochisciopsis* cf. *tetraspora*
27 cf. *Pseudochlorella*
28 *Elliptochloris reniformis*
29 *Chlorella* cf. *homosphaera*
30 *Chlorella* cf. *minutissima*
31 *Muriellopsis* cf. *sphaerica*
32 *Pseudococcomyxa simplex*
33 *Scotiellopsis terrestris*
34 *Gloeocystis papuana*
35 *Coccomyxa gloeobotrydiformis* var.
36 cf. *Oocystis minuta*
37 *Coccothrix* cf. *chlorolobata*
38 *Klebsormidium flaccidum*
39 *Klebsormidium elegans*
40 *Stichococcus* cf. *bacillaris*
41 *Stichococcus* cf. *mirabilis*
42 *Raphidonema nivale* .
43 *Mesotaenium chlamydosporum* var. *chlamydosporum*
44 *Mesotaenium macrococcum* var. *macrococcum*
45 cf. *Mesotaenium*
46 *Cylindrocystis brebissonii* var. *minor*
47 *Cylindrocystis crassa* cf. var. *elliptica*
48 *Cosmarium decedens* var. *decedens*
49 Zygnemataceae sp 1
50 *Microthamnion strictissimum*

Heterokontophyta

51 *Stauroneis* cf. *prominula*
52 cf. *Achnanthes*
53 Xanthophyceae sp 1

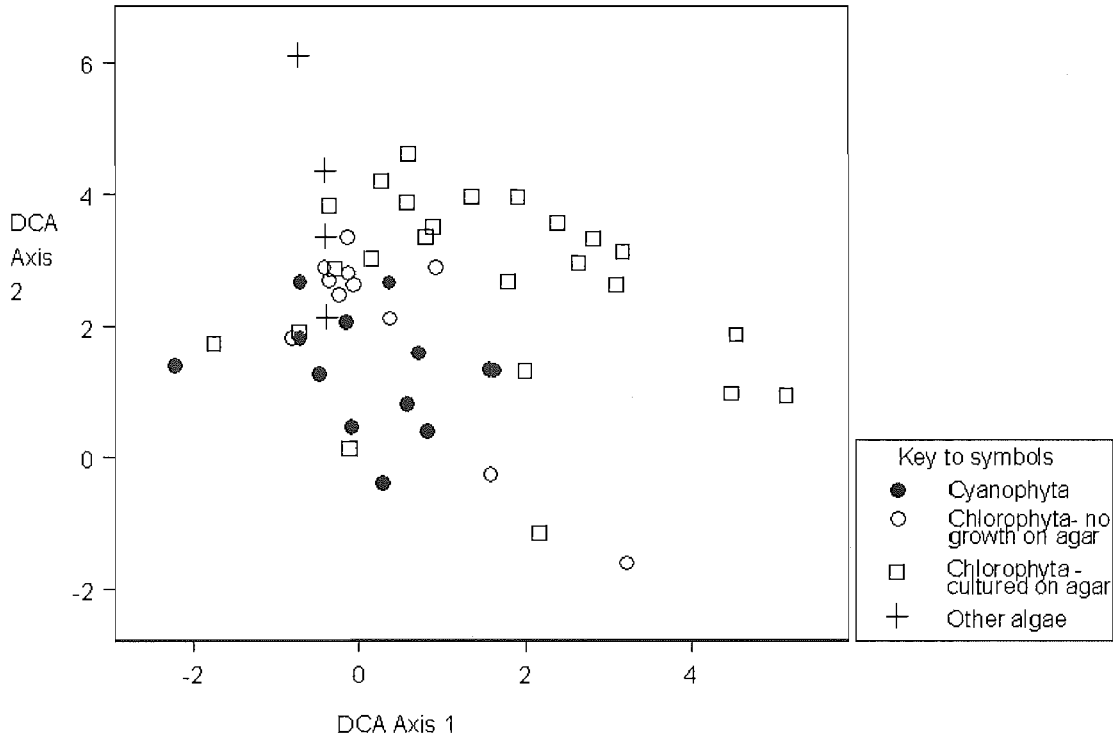


Fig. 3.3.11. DCA results from presence/absence data grouping species according to habitats and highlighting cyanophytes, chlorophytes (with and without growth on agarised culture medium) and algae from other divisions.

Chlorophytes which did not grow on agarised BG-11 medium generally grouped closest to cyanophytes (Fig. 3.3.11, Table 3.3.2) whilst most chlorophytes which grew in BG-11 formed a distinctly separate cluster. Heterokontophytes and *Euglena* cf. *pisciformis*, which also did not grow on this medium, generally grouped in the same region.

3.3.6. Algae present in newly exposed habitats

In 1998, snow algae cysts were almost the only algae detected in snow. Also, they were usually detected on the underlying substratum following snow retreat (Table 3.3.3). Snow algae cysts were present in 31 out of 34 snow samples and 19 out of 34 samples of underlying substratum. Other algae occurred on the underlying substratum in 10 out of 33 samples but, except for *Cyanothece aeruginosa* on 28 November, they were not found in the snow using direct microscopic examination. Cf. *Ammatoidea* and *Fischerella* sp. cell contents were bright blue-green and tapered apices of the former

Table 3.3.3. Algae observed by direct microscopic examination of samples from the edge of retreating snowfields and adjacent exposed substrata, 1998-99 study period.

Site[1]	28 Nov				2 Dec				17 Dec				25 Dec				1 Jan			
	SN		SUB		SN		SUB		SN		SUB		SN		SUB		SN		SUB	
	C	O	C	O	C	O	C	O	C	O	C	O	C	O	C	O	C	O	C	O
1	+	-	+	-	+	-	-	-	+	-	+	-	+	-	-	-	+	-	-	-
2	+	-	+	-	-	-	-	-	+	-	+	-	+	-	-	-	+	-	-	-
3	+	-	+	-	+	-	-	-	+	-	+	-	+	-	-	-	+	-	-	+
4	+	-	+	-	+	-	+	+	+	-	+	+	+	-	+	+	-	-	+	-
5	+	-	-	+	+	-	+	+	M	M	M	M	M	M	M	M	M	M	M	M
6	+	-	+	-	+	-	-	-	+	-	-	-	+	-	-	-	+	-	+	-
7	+	-	+	-	+	-	L	L	+	-	+	+	-	-	+	-	M	M	M	M
8	+	+	-	+	+	-	+	+	+	-	+	+	M	M	M	M	M	M	M	M
T	8	1	6	2	7	0	3	3	7	0	6	3	5	0	2	1	4	0	2	1

[1] For locations, see Chapter 2.
Key to abbreviations: SN=snow, SUB=adjacent substratum, C=red snow algae cysts, O=other algae, M=snowfield completely melted, L=sample lost, T=Total number of sites at which algae were observed.

were frequently absent, as is seen in growing trichomes in culture. The snow algae cysts were always red spheres surrounded by mineral material.

3.3. Discussion

3.4.1. Species richness and composition of communities in different habitats

Distribution of habitats. Growth environment becomes more restricted with higher altitude on Mt Philistine (Table 3.3.1). The only habitats present in all three basins were mineral fines, pools, rock surfaces and *Andreaea* moss. All these contain algae, although rock surfaces support fewer species (Table 3.3.2, Fig. 3.3.1, 3.3.3, 3.3.4). The absence of vascular plants in the upper basin and most of the middle basin (Table 3.3.1) probably reflects low temperatures, more persistent snowcover and high windspeeds. Clearly the lower basin on Mt Philistine has a greater range of habitats for algal growth and would be expected to contain a greater range of species.

In the absence of large bird and mammal populations like those in some Antarctic sites (e.g. Broady 1989b), melting snow in spring may provide the only significantly nutrient-enriched habitat on the mountain, especially since organic soils are so sparse (Table 3.3.1). Initial fractions of snow meltwater are higher in nutrients than the bulk snow (see Chapter 4), although this effect is reduced as the season progresses (Johannessen and Henrikson 1978). The visual appearance of cells of *Fischerella* sp. and cf. *Ammatoidea* (section 3.3.6) suggests that vigorous growth occurs in irrigated substrata.

Water availability is probably the most restrictive factor for growth of algae on Mt Philistine. The importance of liquid water for growth of snow algal populations is discussed in Chapter 4. Moss communities, an important habitat for algae on the site, grow much more profusely in water channels than on exposed surfaces (Fig. 3.3.1e). Although the region receives a very high rainfall (see Chapter 2), water availability in most habitats is potentially limiting, because most areas have little or no soil and are extremely well drained (Fig. 3.3.1). Whenever rain is not falling, drying is rapid. This is especially so on rock surfaces, which, together with snow, support the lowest species richness of all habitats (Table 3.3.2, Fig. 3.3.3, 3.3.4).

Snow. Red, spherical snow algae cysts were present in most habitats, but especially in snow and pools (Table 3.3.2). Their frequent occurrence in pools may be because many were formed initially from melting snow. The species composition of snow is distinct from other habitats except some pool samples (Fig. 3.3.6, 3.3.7). The snow-covered tarn in which large populations develop (see Chapter 4) was not within the randomly chosen sampling squares. These populations are dominated by *Chlainomonas kolii*, which was recorded only once in snow samples collected for this distribution study.

Some snow algae, such as *Raphidonema nivale*, are believed to be facultative, and thus able to grow in habitats other than snow (Hoham 1973, 1980, Ling and Seppelt 1998). Although *R. nivale* was found in 60% of Mt Philistine snow samples, it was never found in other habitats by any detection method (Table 3.3.2), even though it is known to grow in the culture medium (Chapter 6) and temperature used (Hoham 1973). The obligate species of snow algae (*Chlainomonas kolii*, *Chloromonas rubroleosa*, *Chloromonas* species 2, 3, 4) were also not found in other habitat samples. The only snow algae cell type found in habitats other than snow was a red sphere covered by mineral particles, as described from Kosciusko National Park, Australia (Marchant 1982). As a cyst it is not an active component of the flora in these habitats, and it is

probably an obligate snow alga of the genus *Chlamydomonas*. Although this morphotype has been found as bloom-forming populations in Mount Cook National Park (personal observations), such extensive growth has not been observed on Mt Philistine. Given its widespread occurrence in habitats other than snow (Table 3.3.2), it is possible that it is deposited onto the site by wind from further afield. This could also explain its low numbers and fairly even distribution in snow. These cysts were also the only snow algae detected in aerobiota collectors (Chapter 5).

Similarly, there was no evidence that algae predominant in other habitats also grew in snow, although many were dispersed there by wind (e.g. *Fischerella* sp., cf. *Gloeocapsa*; see Chapter 5). Certainly some of them remained viable, as shown by the recovery of *Stichococcus* cf. *bacillaris* into culture from all snow samples (Table 3.3.2). The viability of this organism in snow gives it the potential to grow there. However, its apparent absence in direct microscopic examination suggests that it grows very slowly, if at all. Although cells may be obscured by particulate material in other types of samples, creating the impression that they are absent in direct microscopic observation, this is unlikely in clean snow where there is much less obscuring material.

Deposition of snow algae cysts onto underlying substrata by melting snow was accompanied by deposition of *Cyanothece aeruginosa* on one occasion at one site (Table 3.3.3). Although this was not observed for other algae in 1998, snowfield surveys in 1999 revealed a much more extensive aerobiota (Chapter 5). Therefore, although these organisms do not grow in snow, they may start to grow following deposition onto underlying substrata when snow algal growth ceases. This implies a seasonal succession of algal growth, firstly by snow algae and then by others, both deposited from retreating snow and in established populations irrigated by snowmelt.

***Andreaea* moss.** The other habitat found to contain a distinct algal species assemblage was *Andreaea* moss (Fig. 3.3.6, 3.3.7). This is of particular importance given the ability of *Andreaea* to colonise harsh environments throughout the site, whereas other plants are confined to lower altitudes (Table 3.3.1). Cyanophytes in particular seem to favour this habitat, with a higher mean species richness per sample relative to chlorophytes than is found in most other habitats (Fig. 3.3.4). Cf. *Gloeocapsa* and *Cyanothece aeruginosa* were found in 93% and 100% of *Andreaea* samples respectively. These two algae are also the two most common cyanophytes in all habitats (Table 3.3.2), which may be due to the ready fragmentation and dispersal of *Andreaea* when dry. *Pseudococcomyxa simplex*, which seems to favour plant surfaces (Table 3.3.2; also

Broady 1989b) was found least frequently on *Andreaea*. Many of the culturable chlorophytes (e.g. the seven most common species) were present at lower frequency in *Andreaea* samples than in other plant samples (Table 3.3.2).

Other habitats. No other habitats contained clearly distinct algal assemblages. Vascular plant communities all had similar species composition (Fig. 3.3.6, 3.3.9). This may be because these habitats are restricted to the same area of the mountain (mostly in the low basin, Table 3.3.1), whereas *Andreaea* is dispersed throughout the site and is therefore exposed to a greater range of environmental conditions. Bryophytes were not found to be useful for distinguishing algal assemblages in Spitsbergen (Oleksowicz and Luścińska 1992).

Rock surface communities were highly variable, as shown by their dispersion across more than 50% of Axis 1 (Fig. 3.3.7). This variability is due to a large number of rare species (compare Fig. 3.3.3, showing relatively high total species richness of chlorophytes, with Fig. 3.3.4, showing low mean species numbers per sample). *Chlorella* cf. *homosphaera* may be the algal partner in a lichen symbiosis, which would account for its frequent occurrence in these samples (Table 3.3.2).

Some samples taken from melt pools grouped with snow samples (Fig. 3.3.6), perhaps because the pools first originated from melting snow. Other pools grouped more centrally and may reflect the collection of airborne material from other habitats by rock hollows in which pools are formed, much like the action of an aerobiota collector (see Chapter 5).

The frequency of occurrence of the most common cyanophytes was reduced in mineral fines, soil and rock surface samples (Table 3.3.2). This may be due to the higher susceptibility of algae in these habitats to freeze-thaw cycles. There are no other obvious distinguishing features of their species assemblages (Fig. 3.3.6-3.3.8).

3.4.2. Associations of algae detected by DCA

The most common species, *Cyanothece aeruginosa*, *Fischerella* sp., cf. *Gloeocapsa*, and *Myrmecia* cf. *irregularis* grouped in the same region of the DCA (Fig. 3.3.10). However, none of these has an identical distribution (Table 3.3.2). Some rare species (<10% occurrence, cf. *Myxosarcina*, *Leptolyngbya* sp.1, *Nostoc paludosum*), which are too seldom recorded for conclusions about their distribution to be made, group in the same area.

Among cyanophytes, those with thick, pigmented mucilage generally dominate the driest sites (Pentecost and Whitton 2000). Rapid drying of habitats on Mt Philistine could therefore account for the frequent occurrence of *Fischerella* sp., cf. *Gloeocapsa*, and cf. *Ammatoidea*, though not *Cyanothece aeruginosa* (Table 3.3.2). Resistance to desiccation is widespread throughout the cyanobacteria, however (Whitton 2000). There is also strong evidence that scytonemin, a pigment in the brown mucilage of cyanophytes, protects against UV damage (Whitton 2000). Levels of UV radiation are relatively high at high altitude sites such as Mt Philistine.

Distribution of desmids as a group appears to be quite closely linked (Fig. 3.3.10). It has been suggested that desmids are not viable aerobiota, except as zygospores, which are infrequently produced (Strøm 1926). If correct, direct observational data should produce an accurate estimation of distribution because cells dispersed into different habitats where they do not normally grow will not appear in cultures to confound the results. However, desmids are well-known to be associated with mosses (Gerrath 1993), from which viable short-distance dispersal is very likely to occur. Desmids on Mt Philistine were frequently found associated with mosses and vascular plants, and *Mesotaenium macrococcum* var. *macrococcum* was confined to these habitats (Table 3.3.2).

No other general patterns of association are evident from the species ordination. Many species, such as *Trochisciopsis* cf. *tetraspora*, *Nostoc paludosum*, *Euglena* cf. *pisciformis*, and *Muriellopsis* cf. *sphaerica*, occur rarely and often mutually exclusively, leading to the large dispersion on the diagram (Fig. 3.3.10).

3.4.3. Comparison of distribution patterns of Mt Philistine algae with those elsewhere

The only widespread Mt Philistine taxon to be shared with the flora of Mt Cook National Park (Wilson 1976) is *Cyanothece aeruginosa*. It was not widespread at Mt Cook, being found only in a single sample from a rock pool in the alpine zone. However, no mosses were collected in that study, whereas all moss samples on Mt Philistine contained *C. aeruginosa* (Table 3.3.2). Other common Mt Philistine algae, *Fischerella* sp. and *Myrmecia* cf. *irregularis*, could perhaps have been identified differently at Mt Cook; however, the only possibilities for this (*Stigonema* sp. and *Chlorella* respectively) were found in only 3 from 38 samples. It therefore appears that species of algae present in the alpine zone varies in different parts of the country. Mt

Philistine, being west of the Main Divide, would have a higher rainfall than most sample sites at Mt Cook, which could explain variation in the flora.

Desmids on Mt Philistine favoured plant surfaces over other habitats (Table 3.3.2), whereas Mt Cook desmids were found mostly in tarns and pools (Wilson 1976). However, the epiphytic habitats were not well represented in the Mt Cook study, and water bodies large enough to be called "tarns" were not sampled on Mt Philistine.

Snow algae cysts were frequently found in habitats other than snow (Table 3.3.2). No snow algae were found at Mt Cook except in the one snow sample collected. Since all the Mt Cook samples were taken during March and April, any snow algae cysts deposited into other habitats may have been redispersed by the wind. However, their absence from pools at snow edges in the nival zone seems surprising. The abundance of *Calothrix* in these samples indicates that benthos was sampled, so perhaps these snow cysts float, as is the case for *Chlainomonas kolii* on Mt Philistine (see Chapter 5: dispersal).

Diatoms have been recorded in high numbers as epiliths in some studies (e.g. Marchesoni 1939, Broady 1979a), although not others (e.g. Fjerdingstad 1965). Diatoms were not recorded from rock surfaces on Mt Philistine (Table 3.3.2). Nienow (1996) suggested that diatoms are not well adapted to "subaerial habitats", the definition of which seems to vary. However, living diatoms are rare in general on Mt Philistine (Table 3.3.2), so no comment can be made regarding their habitat preferences. Many studies of epilithic habitats in the European Alps have been made on limestone, which has a high reflectivity, and therefore lower temperature and rate of evaporation of surface water, than other rock types. Water on limestone would also be expected to have a high concentration of Ca^{2+}, and a higher pH. The rock on Mt Philistine is a type of sandstone (see Chapter 2); however, it is not known if different physical properties associated with rock types affect biota (Pentecost and Whitton 2000).

Cf. *Ammatoidea*, the most common of the Mt Philistine Oscillatoriaceae, was found in more than 50% of samples in only *Andreaea* moss and pools. Dominance of Oscillatoriaceae in mosses and ponds is also recorded in several Antarctic studies (e.g. Broady 1987, 1989b). Unlike these studies, dominance of Oscillatoriaceae on Mt Philistine does not extend to other habitats, where cf. *Gloeocapsa* and *Fischerella* sp. are more common (Table 3.3.2). Arctic Oscillatoriaceae are thought to dominate in alkaline conditions (Novichkova-Ivanova 1972); however, the pH of the habitats sampled on Mt Philistine is unknown.

A particularly high species richness has been recorded in mineral fines on Signy Island, Antarctica (Broady 1979a). Mineral fines on Mt Philistine recorded the second highest total species richness (Table 3.3.2), although mean species richness per sample was similar to most other habitats (Fig. 3.3.4).

Presence of *Cyanothece aeruginosa*, *Stichococcus bacillaris* and *Pseudococcomyxa simplex* in mineral fines, as epiphytes on moss and in free-living associations with lichens is similar to findings in Marie Byrd Land, Antarctica (Broady 1989a). However, on Mt Philistine these organisms did not dominate the habitats, *Myrmecia* cf. *irregularis* being the most common alga in all three.

Differences in algal species composition between bryophytes and other habitats have been found in other areas. For example, Arctic mosses tend to have a reduced xanthophyte flora compared to other habitats (Novichkova-Ivanova 1972). Differences between moss types have also been demonstrated, as between *Andreaea* communities and *Polytrichum-Chorisodontium* moss turves on Signy Island (Broady 1979a). On Mt Philistine, *Andreaea* supports a distinct algal community, which differs from that of vascular plants.

Comparison with results from the Kaffiöyra Plain, Spitsbergen (Oleksowicz and Luścińska 1992) is interesting. Using ordination, these authors found that bryophytes were not useful in separating groups of algae. However, they did not use cultures, and the *Andreaea* and vascular plant samples on Mt Philistine are partly distinguished by the diversity of cultured algae in the latter samples (Table 3.3.2). Also, Oleksowicz and Luścińska (1992) found desmids scattered throughout the habitats sampled, whereas Mt Philistine desmids tend to favour plant surfaces (Table 3.3.2).

Certain habitat types sampled in polar studies were absent from Mt Philistine. For example, Antarctic snow algae are often abundant in sites fertilised by excreta from birds and mammals (e.g. Broady 1989b, 1996), and this type of enrichment can also select different assemblages of chlorophytes and diatoms in other habitats (Broady 1987). Obviously, the influence of sea spray (Broady 1989a, Ling and Seppelt 2000) is absent. The flora of persistent streams of varying steepness and velocity has been studied in Antarctica (Broady 1989a), but streams on Mt Philistine occur only in the low basin and are very transient, relying on persistent rain and snowmelt.

3.4.4. Methods used in the detection of algae, and problems of interpretation

The three methods used to examine samples detected different algae with

different degrees of efficiency (Table 3.3.2). Some algae were unique to agarised medium (e.g. *Raphidonema nivale*, *Chlamydomonas* cf. *noctigama*, *Myrmecia* cf. *biatorellae*) while many were never detected by this means (e.g. the desmids, *Chlainomonas kolii*, *Cyanothece aeruginosa*, cf. *Gloeocapsa*, cf. *Ammatoidea*, *Fischerella* sp.). As noted above, these two groups have a different distribution (Fig. 3.3.11).

An obvious question arising from this result is: are the different groupings on the ordination diagram (Fig. 3.3.11) due to distinct distribution patterns or to artificial effects of the different detection methods? Growth on agarised medium indicates that an organism was present in the sample as a viable propagule, but does not necessarily indicate that it was an active component of the community in the habitat from which it was sampled (Broady 1996). Conversely, detection in direct microscopic examination of samples indicates that an organism was present in large enough abundance or size to be visible, but does not necessarily mean it was a viable individual.

Results obtained from enrichment cultures can be used to resolve the latter dilemma. All the common cyanophytes (present in more than 15% of all samples) and the desmids, none of which grew on agarised medium, grew in enrichment cultures (Table 3.3.2). This demonstrates that at least some of the cells were viable. However, many of the most common chlorophytes (present in more than 25% of all samples) were far more prevalent on agarised medium than in enrichment cultures. Although some were probably simply not recognised in enrichment cultures, it is likely that many were grown from viable propagules which were inactive in the habitats from which they were isolated. It has been suggested that development of genetic probes for use in the field may be necessary to overcome this problem (Nienow 1996). This topic relates to dispersal, and is discussed further in Chapter 5.

Although interpretation of results from agarised cultures are complex, they are absolutely necessary to accurately identify most unicellular chlorophytes. Otherwise, those recorded in direct observations and enrichment cultures have to remain as "unidentified unicells". Also, the enrichment culture technique used in this study is not suitable for snow or rock surface samples.

3.4.5. Effectiveness of the ordination procedure

In this instance, rare species had the most influence on separating sample sites in the DCA (Fig. 3.3.6). Common species, by definition, will not distinguish sample sites

when presence/absence data is used. Thus if rare species are removed from the analysis, although the axes will explain more variation, patterns in sample site groupings will not be distinguished.

Rock surface habitats had a strong influence on the DCA (Fig. 3.3.6, 3.3.7). This is due to their frequent occurrence on the site (Table 3.3.1), high total species richness (Fig. 3.3.3), but low mean species richness per sample (Fig. 3.3.4). Although *Myrmecia* cf. *irregularis* and *Chlorella* cf. *homosphaera* were often cultured from rock surface samples, the next ten most common species were not present in more than 15% of all samples (Table 3.3.2). Therefore, epilithic growths include a large number of relatively rare species.

This situation is a consequence of using presence/absence data in the ordination, and arises because the similarity or dissimilarity between rare species will appear to be high, depending on whether they occur together or separately. It has caused some authors to view presence/absence data to be unsatisfactory for comparing species composition between communities (Greig-Smith 1983, Digby and Kempton 1987). Furthermore, high diversity or species richness is not always associated with high biomass (Elster *et al.* 1999), meaning that interpretation of habitat favourability using presence/absence data can be misleading. However, comparable quantitative data would be very difficult to obtain for all the habitats investigated on Mt Philistine, due to their different physical properties. Relative numbers, an alternative to presence/absence data for comparisons between sites, has been found to give less satisfactory ordination results than presence/absence (Allen 1971).

To give some perspective to the ordination diagram (Fig. 3.3.6 – 3.3.9), the range of the first axis from 0.0 to 4.0 indicates that habitats placed at opposite ends should have mutually exclusive species composition. It also shows that species composition of rock surface samples are highly variable.

3.4.6. Summary

Algae are found in all recognisable habitats at the study site. One group, including cf. *Gloeocapsa*, *Cyanothece aeruginosa*, *Fischerella* sp., and *Myrmecia* cf. *irregularis*, are widely distributed throughout the site. Certain other species, such as cf. *Ammatoidea* and red snow cysts, are very common in certain habitats.

Snow and *Andreaea* moss habitats appear to contain distinct algal assemblages. A group of algae including the desmids has a restricted distribution that may be related to similar ecological preferences within the group.

It is likely that recognition of distribution patterns using ordination of presence/absence data is limited by the problem of detection of culturable propagules which are not always active components of communities, and the disproportionate weight given to rare species in analysis of results.

CHAPTER 4.

ECOLOGY OF SNOW ALGAE

4.1. Introduction

4.1.1. Background information on snow algae

"Coloured snow", caused by blooms of snow algae, was first recorded by Aristotle about 400 BC (Fjerdingstad *et al.* 1974). It has now been reported on all continents except Africa (Thomas and Broady 1997). The most commonly reported colour is red (Thomas and Broady 1997), although in some areas, such as Japan, green snow is more common (Fukushima 1963). Other colours reported world-wide include pink (Ling and Seppelt 1990), orange (Garric 1965, Thomas and Broady 1997), yellow (Garric 1965, Thomas and Broady 1997, Kol 1972), yellow-green (Kawecka 1986), blue (Garric 1965, Kawecka 1986), black (Garric 1965), purple (Garric 1965, Kawecka 1986), and grey (Ling and Seppelt 1990). Generally, green snow is caused by actively dividing cells, whereas other colours are caused by resting cells which accumulate secondary pigments (Hoham 1987). Not only may different species cause different or the same colours, but one species, or even one life stage of a species, can cause different colours (e.g. Hoham *et al.* 1979). On Signy Island, Antarctica, red-coloured cells tend to determine snow colouration even when other cell types are far more numerous, due to the intensity of the red pigments (Fogg 1967).

Some snow algae, such as *Raphidonema* and *Koliella*, are believed to be facultative, also being able to grow in soil (Hoham 1973). These algae have a simple life cycle in which only asexual reproduction of a single cell type is known. Chlamydomonadaceae, however, frequently dominate the snow microflora. These are usually obligate, with complex life cycles suited to the transient nature of their growth environment (Hoham 1980, Jones 1991, Thomas and Duval 1995). The vegetative state of the organism is a swimming zoospore, which germinates at the start of the growth season from a resting cyst located beneath the snowpack from the previous winter, and migrates to the snow surface, where asexual reproduction occurs. The growth season, often as short as two weeks (Hoham 1975), concludes by production of new resting cysts, which are typically ornamented, and may be produced sexually or asexually (Hoham *et al.* 1983). Light intensity and wavelength are important in determining when sexual reproduction occurs, at least in certain species (Hoham *et al.* 1997). Cleavage of these cysts into daughter cells, without spore release, may occur in the autumn, but otherwise the cyst remains dormant until the following spring.

The prevalence of resting cysts in these life cycles has led to many incorrect classifications of snow algae, probably including all species of *Scotiella*, *Trochiscia*, and *Cryocystis* which occur in snow (Hoham 1975, Hoham and Mullet 1977, Hoham *et al.* 1979, 1983). Further background to taxonomic problems and approaches to resolving them is presented elsewhere (see Chapter 6: Taxonomy).

Ecology of snow algae is intimately linked with their life cycles, because changes in life cycle stage during the season is undoubtedly a response to changes in the environment. Which environmental conditions are utilised by the cells for their brief growth period? How do the cells change their environment during growth? What determines when the growth period starts, and when it ends? Progress made in answering these questions is outlined in the following sections.

4.1.2 Overview of snow algae ecological studies

The snow environment where algae grow is complex and variable depending on location and time. Much information acquired to date has been obtained in forested areas of North America (Hoham 1971, 1974a,b, 1975, 1976, Hoham and Mullet 1977, Hoham *et al.* 1979, 1983, 1989, 1993, 1997, Jones 1991, Gamache 1992, Bidigare *et al.* 1993). New Zealand apparently has a higher spring and summer snowline relative to the treeline than in North America (see Chapter 2), and thus the snow algae populations are less affected by tree litter and shade on snow. Snow algae in New Zealand are subject to quite different conditions, therefore, than those which have received most attention in the past.

Field conditions in Antarctica might be expected to most closely resemble those of the alpine environment in which New Zealand snow algae are found. Although excellent taxonomic work, often accompanied by ecological observations, has recently been completed in Antarctica (Ling and Seppelt 1990, 1993, 1998a, b, Ling 1996), specific ecological study of snow microbes is more sparse. The major examples of such work are the studies of Fogg (1967), Akiyama (1979) and Ohtani *et al.* (1998).

North American studies involving open (treeless) areas include those of Thomas (1972), Mosser *et al.* (1977), Hoham and Blinn (1979), and Thomas and Duval (1995). Although the influence of wind-deposited material from trees may still be considerable due to close proximity to the treeline, these studies provide illuminating results when considering the conditions to which New Zealand snow algae may be exposed.

A major difficulty associated with investigating the ecology of snow microbes can easily be illustrated. Many authors have reported the concentration of nutrients in bulk snow samples where algae were present (Thomas 1972, Komarek *et al.* 1973, Kol and Eurola 1974, Gerrath and Nicholls 1974, Hoham and Mullet 1977, Hoham *et al.* 1989, Gamache 1992, Ohtani *et al.* 1998, Mueller *et al.* 1998b). However, snow algae grow in meltwater spaces between the crystals (Jones 1991). The concentrations of nutrients in meltwater may vary considerably from bulk snow concentrations (Johannessen and Henrikson 1978, Cadle *et al.* 1984, Davis 1991). All environmental data relevant to snow algae growth in the field suffers from the inability to isolate this habitat for measurements. As a consequence, much knowledge of growth preferences of snow algae applies to cultured populations.

4.1.3. Light

Light is thought to be the most important factor influencing distribution of snow algae (Hoham 1984). For example, Fukushima (1963) found *Chlamydomonas* to dominate medium to low insolation sites in Japan, whereas *Ochromonas smithii* (a Chrysophycean) was prevalent in high insolation sites. Hoham and Blinn (1979), in a survey of the cryoflora of the American Southwest, found that *Chlamydomonas nivalis* (Bauer) Wille was the dominant species in open-exposed slopes, but was replaced by *Chloromonas nivalis* (Chodat) Hoham & Mullet in shaded areas.

Other snow algae which are not reported to occur on open/exposed slopes above the treeline include *Gymnodinium pascheri* (Suchlandt) Schiller (Gerrath and Nicholls 1974), *Chlainomonas rubra* (Stein & Brooke) Hoham (Hoham 1974a), *Chlainomonas kolii* (Hardy & Curl) Hoham (Hoham 1974b), *Chloromonas pichinchae* (Lagerheim) Wille (Hoham 1975), *C. brevispina* Hoham Roemer & Mullet (Hoham *et al.* 1979) and *C. polyptera* Hoham Mullet & Roemer (Hoham *et al.* 1983).

Snow algae can survive extremes of light, having been found in conditions of less than $1.1x10^3$ lux to greater than $1.1x10^6$ lux (Hoham 1971). Light intensities were initially thought to be directly responsible for the development of red pigments in snow algae (e.g. Hoham 1971, Fjerdingstad *et al.* 1974). It now appears that the situation is more complex, and involves levels of combined nitrogen in the snow (see 4.1.6). It is certain that the same species may be responsible for different coloured snows (e.g. Hoham *et al.* 1979). Phototactic response has been documented for *Chloromonas pichinchae* (Hoham 1975).

Vertical distribution of *Chlamydomonas nivalis* in response to light was studied by Grinde (1983). Cells descended as much as 16 cm through the snowpack after 8 hours sunlight, during which time the position of those that were shaded did not change. Fogg (1967) studied vertical distribution of algae in snow at Signy Island, Antarctica, but concluded that apparent increases in concentrations of cells in certain layers were the result of snow ablation.

Hoham *et al.* (1997) studied the effect of different light regimes on gametogenesis and mating in *Chloromonas* sp.D. More mating between two compatible strains occurred under blue light, and light intensity affected mating orientation of cells. However, more mating occurred under high intensity red light than under low intensity blue light, suggesting a complex interaction between light intensity and wavelength. Therefore, quality of light plays a role in reproduction of some snow algae.

4.1.4. Temperature

The temperature range of 1-4°C seems to be typical of flagellate snow algae growth optima in culture (e.g. Hoham 1974a, 1975, Kawecka and Drake 1978, Hoham and Blinn 1979, Hoham *et al.* 1983, Ling and Seppelt 1993). Survival (viability for culturing) of snow algae at very low temperatures has also been studied. Vegetative cells of *Mesotaenium berggrennii* (Wittrock) Lagerheim can survive temperatures as low as -25°C (Ling and Seppelt 1990), and aplanospores of *Chlamydomonas nivalis* are viable after dark freezer storage from one month (Kawecka 1981) to one year (Fjerdingstad *et al.* 1974).

Thomas (1972) reported that photosynthetic rate was high in *Chlamydomonas nivalis* at low temperatures ("surface unmelted snow") but was inhibited by even slight melting (an increase of no more than 5°C which is, however, beyond the range of most culture temperatures, as shown above). Mosser *et al.* (1977) also found high photosynthesis rates at low temperatures, but wide variation in optimal temperatures between populations, and optima considerably higher than ambient snow temperatures. Optimal temperature for photosynthesis in most melted field samples was 10-20°C, but exceptional peaks occurred at 0°C and -3°C.

Variation in optimal temperatures for photosynthesis has been explained by algae adapting to a wide range of temperatures through their exposure to environments other than snow (Mosser *et al.* 1977). For instance, resting spores of snow algae may be

deposited on soil or rock by melting snow, requiring survival of high temperatures, desiccation and increased light levels (Hoham *et al.* 1989).

The effect of temperature reduction on ^{86}Rb uptake (a K^+ substitute) was found to be less in *Chlamydomonas nivalis* than in *C. reinhardtii* Dangeard, a temperate species sensitive to both freezing and chilling (Clarke *et al.* 1986). Some snow algae have been shown to have specific structures on their cell membranes that appear to be linked to their tolerance of cold temperatures (Clarke and Leeson 1985). Active uptake of substrates by microbes is severely impaired at low temperatures (Nedwell 1999), possibly due to a loss of membrane fluidity at low temperature, which prevents conformational changes necessary for transporter proteins to function. The result is a decrease in affinity for substrates with decreasing temperature, implying that even a relatively high concentration of substrate in a given environment at low temperature cannot be assumed to indicate that the organisms present are not substrate-limited (Nedwell 1999).

4.1.5. Quantity of interstitial water in snow

It is generally accepted that snow algae do not appear in the field until air temperature continuously exceeds 0°C, when a continuous meltwater supply is present in the snowpack (e.g. Fukushima 1963, Hoham 1971, Yoshimura *et al.* 1997). Snow algae in forested areas are often found in parallel horizontal bands containing the wettest snow (Hoham 1971). This could be a result of cell transportation by water, or due to the tendency of nutrients to accumulate in such layers (Brimblecombe *et al.* 1985). Liquid water flowing laterally or gravitationally through a snowpack is probably important for nutrient supply to snow algae (Hoham 1975).

In correlating the water equivalent of snow with field observations of algae in the snowpack, it was suggested that light and (or) meltwater may be key factors initiating germination of *C. pichinchae* zygotes (Hoham 1975). Cells of flagellate snow algae require liquid melt water in order to swim (e.g. Hardy and Curl 1972, Hoham 1974a). Hoham *et al.* (1983) correlated *Chloromonas polyptera* cell types with waterflow and snow water equivalent data and suggested that higher light intensities and possibly a more water-saturated snowbank were required for the germination of *C. polyptera* zygotes than for those of the previously studied *Chloromonas* species.

Ling and Seppelt (1990) used the method of Hoham (1975) to measure snow water equivalent (the volume of melt divided by the volume of the snow giving rise to

the melt) during collection of *Mesotaenium berggrennii* in Antarctica and recorded values of 42-53%. Nothing was concluded other than that this was at the lower end of ranges recorded by Hoham in the USA. Snow water equivalent has sometimes been referred to as water content (e.g. Hoham 1975, Hoham and Mullet 1977). This is rather inaccurate terminology because completely dry or frozen snow will still give a reading greater than zero. In this thesis liquid water content (LWC) of snow refers to the proportion of snow mass which is liquid water at a particular time (thus a frozen snow sample has LWC of zero, but will still have a water equivalent measurable by the formula above).

Comment regarding the importance of liquid water has been extensive. It is also implicated by definition in the generally accepted theory applied to the life cycle of flagellated snow algae, in which flagellated cells swim upwards through the snow after germination. It therefore seems surprising that such a variable has not received more attention. However, although some technically straightforward, but time-consuming, techniques exist (e.g. Davis and Dozier 1984), electronic probes capable of measuring snow LWC efficiently have been developed only relatively recently (e.g. Denoth *et al.* 1984), and their availability may have been limited.

4.1.6. pH

Snowmelt from the comparatively pollutant-free ice sheets of Antarctica and Greenland typically has a pH of 5-6 (Mellor 1977). Ling and Seppelt (1993) recorded pH ranges from 4.6-6.2 in snow from Windmill Islands, continental Antarctica, containing *Chloromonas rubroleosa* Ling & Seppelt. The pH of New Zealand snow may be similar as it is also less anthropogenically affected than snow in the USA (Wilson 1959a, b). However, typical pH and its spatial and temporal variability in New Zealand snow is unknown.

The first research linking snow chemistry with occurrence of snow algae was the investigation of snow pH. Kol (1934) developed a "silicotroph - calcitroph" hypothesis, relating incidence of snow colour caused by algae to different rock types underlying the snow. This was later developed into a hypothesis relating distribution of red snow to pH 4.5-5.8, and other colours to above pH 5.7 (Kol 1968b). However, the data supporting this suggestion have been described as "controversial" (Hoham 1971). There is also contradictory evidence. Japanese (Fukushima 1963) and north-west USA (Garric 1965) distributions of red and green snow are related to their sun exposure

rather than underlying rock. *Gymnodinium pascheri* was found forming red snow with pH 7.1 (Gerrath and Nicholls 1974). Hoham (1980) stated that it was still unknown whether distribution of individual species of snow algae was influenced by pH. There are large errors associated with measuring the pH of acidic solutions of low ionic strength (Brimblecombe *et al.* 1985, Tranter *et al.* 1987), and the pH of an aqueous solution changes with temperature (Clarke *et al.* 1986), both of which complicate the interpretation of field data.

Snow in North America is frequently contaminated by acid precipitation (e.g. Hoham and Mohn 1985). Environmental concerns have therefore dominated later investigation into the effect of pH on snow algae.

The chrysophycean snow alga *Chromulina chionophila* only appeared in initial cultures at a pH below 5 (Stein 1963). The alga was collected from a site where the snowmelt pH was 4. Optimal pH ranges for growth on M1 medium were found to be 4.0-5.0 for an Adirondack *Chloromonas* species and 4.5-5.0 for *C. polyptera* from Arizona (Hoham and Mohn 1985). However, different responses on AM medium prompt caution in relating the pH optima in culture to those in the snowpack. Hoham *et al.* (1989) suggested that acid precipitation is selecting acidophilic strains in the Adirondack Mountains, USA.

4.1.7 Nutrients

Nutrient sources for snow algae are reported to include litter falling on snow and atmospheric dust deposition (Hoham 1980). Capillarity from soil is unlikely to be a factor once the snow LWC is greater than about 1%, as water movement then occurs by gravitational percolation (Langham 1981). Rain is undoubtedly capable of adding nutrients to snow (Barry and Price 1987).

Snow from beneath conifers stimulated more growth of *Chloromonas pichinchae* than snow from open areas when meltwaters were used in media (Hoham 1976). More dissolved reactive phosphorous (DRP) was also found in snow beneath conifers, and Hoham (1971) had previously found that growth rates of *Chlamydomonas*, *Raphidonema*, and *Cylindrocystis* species on snowmelt from different elevations correlated well with levels of DRP in the melt.

A positive response occurred when *Chloromonas pichinchae* was grown on extracts of coniferous leaves, bark, and pollen, compared to media lacking these extracts (Hoham 1976). Positive, neutral and negative responses were all recorded for

Raphidonema nivale under the same conditions. In the field, *C. pichinchae* was more abundant under coniferous canopies than in snow from other areas.

A number of studies measured nutrient content of snow samples at the site of collection (e.g. Thomas 1972, Kol and Eurola 1973, Komarek *et al.* 1973, Gerrath and Nicholls 1974, Hoham and Mullet 1977, Mueller *et al.* 1998, Ohtani *et al.* 1998). A comparison between the measurements obtained in these and the present study is provided in the discussion (section 4.5.4). There is so much variation in reported values that "typical" concentrations of any nutrient are difficult to suggest. Fogg (1967) and Kawecka *et al.* (1979) suggested caution in interpreting such data in relation to algal abundance, because a high number of cells at a given site may be a result of concentration due to snow ablation rather than cell proliferation as a response to nutrient levels. Also, nutrient levels in a snowpack can change after short periods of time, since they may be altered by ablation or rainfall (Hardy and Curl 1972).

Levels of combined nitrogen in snow have now been implicated in production of the red astaxanthin pigment in some snow algae. Bidigare *et al.* (1993) hypothesised that pigment production is a response to high irradiance under low nitrogen conditions. There is circumstantial evidence supporting this from Antarctica, where green snow frequently occurs near penguin rookeries but red elsewhere (Broady 1989b). Thomas and Duval (1995) and Bidigare *et al.* (1993) found convincing evidence that the red pigment has a photoprotective function. Czygan (1970) showed a pigment shift in *Chlamydomonas nivalis* resting cells placed in nutrient broth for 4 weeks. However, Czygan's experiment was conducted under light intensities of 6000 lux in the laboratory, far less than those recorded in the field (e.g. $70x10^3$ lux by Thomas and Duval 1995). Thus the pigment shift could have been due to lower light levels in the laboratory rather than increased nutrient supply (Hoham 1980). Nevertheless, Hoham (1987) stated that biosynthesis of red pigment in *Chlamydomonas nivalis* parallels chlorophyll decomposition and nitrogen deficiency in snow, presumably based on this data. Red snow samples on King George Island, Antarctica, had lower averages and ranges of NH_4-N and DRP concentrations than green or brown snow, although there was considerable overlap (Ohtani *et al.* 1998).

Hoham (1971) considered that nutrient concentrations in snow are likely to be depleted by vegetative populations until resting spores form, and also that NO_3-N would be the first limiting nutrient. This implies that NO_3-N may be important in determining shifts in life cycle stages. A decrease in NO_3-N utilisation in snow from the Laurentian Mountains, Quebec, has since been correlated with the shift from a vegetative

Chloromonas cell type to a sexually produced resting stage (Hoham *et al.* 1989). Similarly, Yoshimura *et al.* (1997) found NO_3-N levels to be generally lower in snow containing algae than in snow with no algae, possibly due to its utilisation by the cells.

Gamache (1992) conducted the most thorough investigation of snow algae nutrition to date. Studying populations of *Chloromonas* sp. in Canadian snow, he found that conductivity and levels of the nutrients NO_3-N, NH_4-N, and SO_4^{2-} were all significantly lower in green than in white snow. Conserved Cl^- concentrations were used as evidence that depleted nutrients were the result of algal utilisation. A rainfall simulator in the laboratory was also used to measure changes in nutrient concentrations in meltwater eluted from a snow column containing algae. However, the possibility could not be discounted that bacteria in the snow, rather than algae, accounted for changes in concentrations observed when simulated rain was passed through the column.

Although Gamache (1992) followed levels of NH_4-N and NO_3-N on a temporal scale, no information on the populations of algae (cell types or numbers, other than an overall average in the samples for nutrient analysis) was obtained. Thus the hypothesis of Hoham (1971), relating nutrient (particularly NO_3-N) concentration to shifts in life cycle stages, remains to be tested more thoroughly.

As mentioned in section 4.1.1, the conditions under which these nutritional studies have been carried out are likely to be quite different from those found in New Zealand. This is due to both forest cover over snow and the high anthropogenic inputs into precipitation in North America. The likely differences in chemistry between North American and New Zealand snow makes an overview of events contributing to snow composition worthwhile. This will also indicate why the heterogeneity of snow is so marked and universally reported.

Snow formation. Snowflakes form when micron and sub-micron sized particles, which may be water-soluble or insoluble, serve as nuclei in clouds (Gunz and Hoffmann 1990). Other particles are collected during snowflake growth, and additional chemical impurities are obtained by scavenging as the flake moves through the atmosphere (Granberg 1985, Gunz and Hoffmann 1990). The scavenging efficiency of a snow crystal increases with decreasing diameter (Schemenauer *et al.* 1981). Most compounds acquired by snow during its deposition are probably found on the surface of snow crystals (Johannessen and Henrikson 1978). Vertical mixing of air masses may play an important role in determining properties and composition of snow because the

characteristics of different air masses impart different shapes and sizes to snow crystals (Granberg 1985).

Oceans as a source of compounds in precipitation. Air transport of sea salt particles is commonly reported. Concentrations of SO_4^{2-}, Na^+ and Cl^- in Californian snow have been linked with sea salt from the west (Gunz and Hoffmann 1990). Similar findings were obtained from Greenland snow (Mayewski *et al.* 1987). Therefore, large water bodies can have a profound influence on chemistry of precipitation onto downwind land masses. However, NH_4-N and NO_3-N in Terre Adelie snow, Antarctica, were thought to have no marine source (Legrand and Delmas 1985); however, this does not follow the hypothesis of Wilson (1959b, see below).

Wilson (1959a) measured the nitrogen content of New Zealand winter snow and found no NO_3-N or NO_2-N. This finding has obvious implications for the hypothesis of Hoham (1971) in the New Zealand setting. These compounds are the classical nitrogen-cycle atmospheric contributions, occurring as fixation products of electrical discharge (Legrand and Delmas 1985). Since HNO_3 is efficiently scavenged by snow (Gunz and Hoffmann 1990), and an important source of this compound in Antarctic snow is believed to be the tropics (Legrand and Delmas 1985), the absence of NO_3-N in New Zealand snow as reported by Wilson (1959a) seems surprising. Instead, most nitrogen in New Zealand snow was found to occur in the organic fraction, at values of up to 230 $\mu g\ l^{-1}$. Wilson (1959a, b) reasoned that the nitrogenous material was sourced from the surface microlayer of the ocean, which is richer in K^+, NH_4^+, organic material and organic nitrogen than bulk ocean water. By plotting the excess K^+ concentration against the organic nitrogen concentration for snowmelt, ocean foam, and ocean water, Wilson (1959b) found that they fell close to a straight line, implying a possible common origin for the compounds in all three water types. If this is the case, transport of water droplets from the ocean to the land via wind and precipitation could amount to several kilograms of nitrogen per hectare per year (Wilson 1959a, b). Therefore, it is possible that compounds could be sourced from the ocean without having the same concentration in precipitation as in bulk ocean water. This could account for conclusions such as those of Legrand and Delmas (1985) that inorganic N in Antarctic snow is not sourced from the Southern Ocean.

Dust and dry deposition. Especially heavy dust contamination may cause coloured snowfalls. One such event, which occurred in the Canadian Arctic, had origins in both

the US and Asia (Welch *et al.* 1991). Wilson (1959a) concluded that terrestrial dust probably did not contribute to the chemical composition of winter snow in New Zealand, based on the absence of insoluble inorganic material and NO_3-N in samples. However, accounts from other areas imply that the degree of dust input into snow varies between years and seasons (Mayewski *et al.* 1987, Wagenbach *et al.* 1988, Gunz and Hoffmann 1990) and that its weathering may reduce the acidity of polluted snow (Delmas *et al.* 1996).

Chemical reservoirs held in snow can be supplemented during winter by wind-blown additions termed "dry deposition". An example of this phenomenon is the dry deposition of sulphur-containing compounds and their subsequent oxidation, which can contribute to acidification of snow (Gunz and Hoffmann 1990). Wagenbach *et al.* (1988) viewed dry deposition of wind-blown particles to be important in delivering impurities to snow surfaces in the Swiss Alps throughout the year.

Anthropogenic inputs. Pollution of snow and rain comes from combustion products of fossil fuels, fumes from industrial processes, dust and spray from road salts, pesticides, and fertilisers, and atmospheric modifications of any of these (Mellor 1977, Berg *et al.* 1991). Increases in acidity and conductivity of snow in the Swiss Alps over the last hundred years are thought to be the result of anthropogenic impact (Wagenbach *et al.* 1988). Gunz and Hoffmann (1990) stated that most nitrogen compounds in the atmosphere are associated with anthropogenic sources. Lovett (1992) found that dry deposition of N was dominated by HNO_3. Anthropogenic sources dominate SO_2 emissions in industrialised areas (Gunz and Hoffmann 1990, Calvert *et al.* 1985).

Pollutants are often trapped in a low layer of air (Wagenbach *et al.* 1988, Gunz and Hoffmann 1990, Berg *et al.* 1991) which may contaminate an upper layer if mixing of the air masses occurs. In the Swiss Alps, anthropogenic trace elements were found to be much higher at lower sites, which were immersed in the polluted mixing layer. Exceptions to this occurred during extreme weather, such as thunderstorms in summer, which caused the mixing layer to rise (Wagenbach *et al.* 1988). In Central and Southern California, air masses passing over industrial areas have given rise to snow that is higher in pollutants than snow which falls from clouds travelling over other areas (Gunz and Hoffmann 1990, Bowman 1992). It also seems that rimed snow can accumulate greater levels of contaminants than unrimed snow (Berg *et al.* 1991, Kalina and Puxbaum 1994).

Seasonality. Studies of South Greenland snow by Mayewski *et al.* (1987) revealed a link between NO_3^-, Cl^-, and ^{18}O (representing temperature). The authors suggested that differences in air moisture content, which varies with temperature, could lead to differences in style and rate of chemical incorporation into snow.

Changes following deposition. The variability of snow on the ground arises not so much from variable origins as from variable conditions once deposited, and because it exists close to its melting temperature (Colbeck 1987). Metamorphism of the snowpack following deposition results in a coarser snow skeleton, with crystals of reduced surface area (Granberg 1985). Also, redistribution of fallen snow by wind results in inconsistent thickness throughout the catchment (Tranter *et al.* 1986). Snow on the ground can be redistributed, depending on topography, by winds as low as 0.15 m s^{-1} (Delmas and Jones 1987). This redistribution to surfaces which are relatively sheltered from erosive forces influences the physical characteristics and chemistry of snow (McKay and Gray 1981, Tranter *et al.* 1986, Pomeroy *et al.* 1991).

A temperature gradient may lead to a redistribution of compounds within dry snow through the physical processes of evaporation from a lower, warmer zone and condensation in higher, colder layers. Snow metamorphism may therefore concentrate surficially adsorbed substances into certain layers (Granberg 1985).

Chemical composition of a snowpack in summer varies due to differences in composition of the individual snowfalls over winter and subsequent leaching and redistribution of solute (Tranter *et al.* 1986). Precipitation can add nutrients to snow following its deposition (Barry and Price 1987). Rain may also increase the variation of nutrient concentrations both horizontally and vertically within a snowpack. The pathway of meltwater and rain through a snowpack is dependent on structural characteristics of the pack, such as ice lenses and stratified snow layers of different density, which have the result of increasing compositional heterogeneity during snowpack evolution (Jones 1987). Furthermore, meltwater percolation is not always uniformly downwards; it often moves laterally within a snowcover and flows down through channels at certain points (Jones 1985, Davis 1991).

Preferential elution of nutrients. Nutrients in snow accumulate during winter and are released in spring (Jones 1991). Johannessen and Henrikson (1978) found that 60-90% of SO_4^{2-}, NO_3^- and NH_4^+ ions in a Norwegian snowpack were washed out within 10 days of the start of melting, during which time the snowpack volume decreased by only

35%. More than 50% of these ions were released in the first 21% of melt in a USA snowpack (Cadle and Dasch 1984). Concentrations of major ions in first meltwaters may be enriched by a factor of 7-10 relative to the parent snowpack in the Turkey Lakes area, Ontario, Canada (English *et al.* 1987). Davis (1991) suggested that, on average, 80% of solutes elute from snow with the first 20% of melt.

Because seasonal snowcovers undergo extensive recrystalisation during metamorphism, most solutes will be redistributed to the outsides of crystals, facilitating their rapid removal during the spring melt (Davis 1991, Tranter 1991). Freeze-thaw cycles cause chemical constituents to segregate from granular snow particles into water spaces, because the chemical constituents of ice segregate along grain boundaries (Suzuki 1982). This produces the concentration effect observed in the spring melt.

This phenomenon is relevant to the study of algae. Gamache (1992) found that a green snow bloom did not appear until the first flush of pollutants (in particular a rise in acidity from contaminating H_2SO_4 and HNO_3) had been lost from the snow in the spring. Preferential elution has usually been studied in polluted systems, where understanding of the effect is desirable from a management perspective. Whether the initial melt period has such relevance to an unpolluted system, such as a New Zealand snow community, is unknown.

In many areas spring melting is not a continuous uninterrupted event. The snowpack may undergo many and variable thaw-freeze cycles, with a constant redistribution of nutrients within it. Consequently a complex time course of chemical fluxes may occur (Barry and Price 1987).

The influence of trees. The work of Hoham (1971, 1976), Hoham and Mullet (1977), Jones (1991), and Gamache (1992) was all conducted in snow systems closely associated with forest. The amount of biological debris deposited on snow is far greater in forests than in open areas. During melt, the material is leached and soluble nutrients penetrate to the upper soil and litter layers. Plants, animals, and microbes influence nutrient pools of snowcover far more in forested areas than on open snowfields (Jones 1991). A greater influence of inorganic processes on snow metamorphism is expected in unforested alpine and sub-polar snowcovers, compared to a forest system where biologically mediated influence is more likely, given the greater content of organic matter in the snowcover (Tranter 1991).

Spatial irregularity in deposition of large amounts of debris causes variations in the physical nature of snowpacks under forest. This can influence meltwater flow and

cause spatial variability in chemical content, especially during rain and melt events. Vertical pipeflows (concentrated areas of meltwater percolation) are prevalent under the dripzones of trees (Jones 1985). The quality of incident snowfall is little affected by a tree canopy, but the quality of snow on the ground is considerably affected by organic debris, drip zones and redistribution of snowfall associated with trees (Jones 1987). Throughfall in a forest can transfer material to the snowpack that was dry-deposited on a canopy (Cadle 1991).

All studies reviewed by Jones (1991) showed that litterfall changes the nutrient pool of the snowcover, and the greatest changes take place during the spring melt period. Litter has been found to contribute more than deposition from the atmosphere to the soluble cationic load of snowcovers, and is effective in reducing the nitrogen pool via microbial growth (Jones 1991).

Trees affect both the distribution of snow and its depth (Jones 1991). Less snow is deposited beneath forest than in open areas at the start of winter (Cadle and Dasch 1984), but the snow generally persists in a forested site for 2-3 weeks longer than in open sites (Jones 1987).

Processes affecting snow on the surface of lakes. Periodic, abrupt thinnings of snowcover occur on lakes due to wind action and flooding several times during winter. The result is generally a thinner snowcover containing steeper subsurface temperature gradients than those found in terrestrial cover. Snow usually becomes integrated with an underlying ice sheet. Stratigraphic development of lake snowcover is likely to be poor, and it will be very spatially variable. Flooding occurs when the ice below the snow cracks and water is drawn up by capillary action, producing a layer of slush at the snow-ice interface (Adams 1981). Nutrients may accumulate in these slush layers (Brimblecombe *et al.* 1985) through the action of freeze-thaw cycles (Tranter 1991).

4.1.8. Aims

Much remains to be discovered in many areas of the study of snow algae. Ecology of New Zealand snow algae is thus far an unexplored field. The differences between the New Zealand snow algae habitat and that of North America, where most ecological research has taken place, have been outlined above, together with the reasons for these differences.

Clearly the Mt Philistine study site provides a new opportunity to study ecology of these microbes in a temperate environment more removed from human influence than most of those studied before. Fundamental questions applying to the Mt Philistine snow algae are as follows.

- What factors influence the time of appearance of the snow algae population each season?
- Do the different types of snow algae found on the mountain have different ecological preferences?
- What resources are available for growth of snow algae on Mt Philistine, and how do they and their utilisation compare with those elsewhere?
- How does resource availability vary between seasons?
- Which nutrients are utilised by snow algae on Mt Philistine? How do populations respond to changes in these nutrients?
- Does preferential elution of nutrients influence growth of snow algae in New Zealand?
- What conditions are suitable for growth? Under what conditions is growth prevented?

4.2. Methods

4.2.1. Logistics and preparation

1998 study period. A preliminary trip to the study site was made on 30 October 1998 to assess conditions. At this time the tarn site (Fig. 2.4, Fig. 2.6e,f) was still completely snow covered, with a small crack forming in the centre which indicated that break-up of the surface was imminent. Samples were taken for preliminary observation from where snow algae were expected to grow. This day constitutes day 0 in results section. A camp (Fig. 4.2.1a) consisting of two tents, field and personal equipment, mountain radio and a kea-proof storage barrel was carried to the snowline at 1590 m on 13 November 1998 (day 13 in results), marking the start of the detailed study period. Assistance in this carry was provided by several members of the Canterbury University Tramping Club (Fig. 4.2.1b). The period of detailed study lasted until 2 January 1999 (day 63), when almost all snow was gone from the tarn. Occupation of the site occurred for

periods of up to 8 consecutive days, except when extended stretches of bad weather (especially winds greater than 100 km h^{-1}) forced a retreat to Arthur's Pass Village.

1999 study period. The preliminary trip to the site was made on 26 October 1999. At this date snow breakup on the tarn surface had reached a relatively advanced stage compared to the previous season, with considerable surface water visible. Equipment was carried to the site alone over 6 repeated trips from 8-11 November (days 1-4 in results). The camp was sited about 30 m higher, in a slightly less exposed position, than in 1998 (Fig. 4.2.1e). The site was occupied for several days at a time in order to take 4 a.m. samples, beginning on 13 November (day 6) when the weather forecast indicated that a major storm was about to begin.

4.2.2. Weather record

Qualitative weather records were collected during each study period. Parameters recorded were:

- incidence of rain during each day.
- incidence of snow during each day.
- presence of cloud, and whether it was continuous or intermittent.
- changes during the day.

4.2.3. Snow level and melting

Snow depth was monitored at the tarn site and in the upper basin during the 1998 study period. In 1999 only the tarn site was used. Depth of snow was measured using a graduated snow stake hammered to rocks underlying the snowpack and left there for the duration of the study. Measurements were taken every 1-2 days (except during bad weather in 1998). Measurements were made by standing the stake upright in its hole (generated by melting) and the marking recorded where a ruler placed on the snow surface on either side of the hole intersected the graduated scale on the stake.

Retreat of eight snowfield edges (see Fig. 2.4 for locations) over time was monitored during the 1998 study period. A small plastic marker was placed at the position of each snow edge and the distance this retreated was recorded every 3-4 days during fine weather.

Melting of snow on the tarn surface was recorded diagrammatically every 7-10 days during the 1998 study period using the snow algae sampling grid as a reference (see 4.2.5).

4.2.4. Environmental parameters

Rainfall. Rainfall was measured using a graduated rain gauge (Fig. 4.2.2a) placed upright between rocks on a snow-free area at the tarn site during the 1999 study period. Measurements were taken every 2 days during the snow sampling period.

Light. Photon fluxes were measured at the surface of several snowfields, including snow on the tarn surface, every 3-4 days during fine weather over the 1998 study period, using a Licor data logger with spherical sensor. Total photon fluxes in surface snow were measured by placing the sensor on the snow surface. Incident photon fluxes were measured by placing the sensor on black non-reflective material at the snow surface.

Incident light intensities were recorded at the tarn site during the 1999 study period using a light meter/data logger (Onsett Instruments Optic Stowaway re-housed in a home built cosine correct and waterproof housing), held upright between rocks on a snow-free area of the tarn shore (Fig.4.2.2a).

Nutrients. Concentrations of NH_4-N, NO_3-N and dissolved reactive phosphorous (DRP) in snow samples were determined colourimetrically (Mackereth *et al.* 1978), using a Jasco Model 7850 spectrophotometer (see Appendix 2 for standard curves). Deionised water (obtained using a Barnstead Nanopure UV ultrapure water system) was used throughout in all reactions. Exceptions to the methods of Mackereth *et al.* (1978) were as follows.

(i) Cells with 10 cm path length were used in the spectrophotometer to enable detection of low concentrations.

(ii) For NO_3-N, cadmium coarse powder was used instead of spongy cadmium.

(iii) For DRP, the lower sensitivity method was used and the volumes doubled so there was enough solution to fill 10 cm cells.

Fig. 4.2.1. Field work, 1998-99: a, campsite 1998 with Mt Rolleston (2275m) in background; b, carrying equipment to site on 12 November 1998; c, tarn snow with grid in place (arrow, squares have 1 m sides, arrowhead to corner stake); d, working on tarn, 27 November 1998, showing safety rope and edge of grid (arrow); e, campsite (foreground) 1999-2000, with Mt Philistine in background (tarn site is above rock wall behind tent); f, g, grid placement and some algal-coloured snow visible near water edge (15 November 1999).

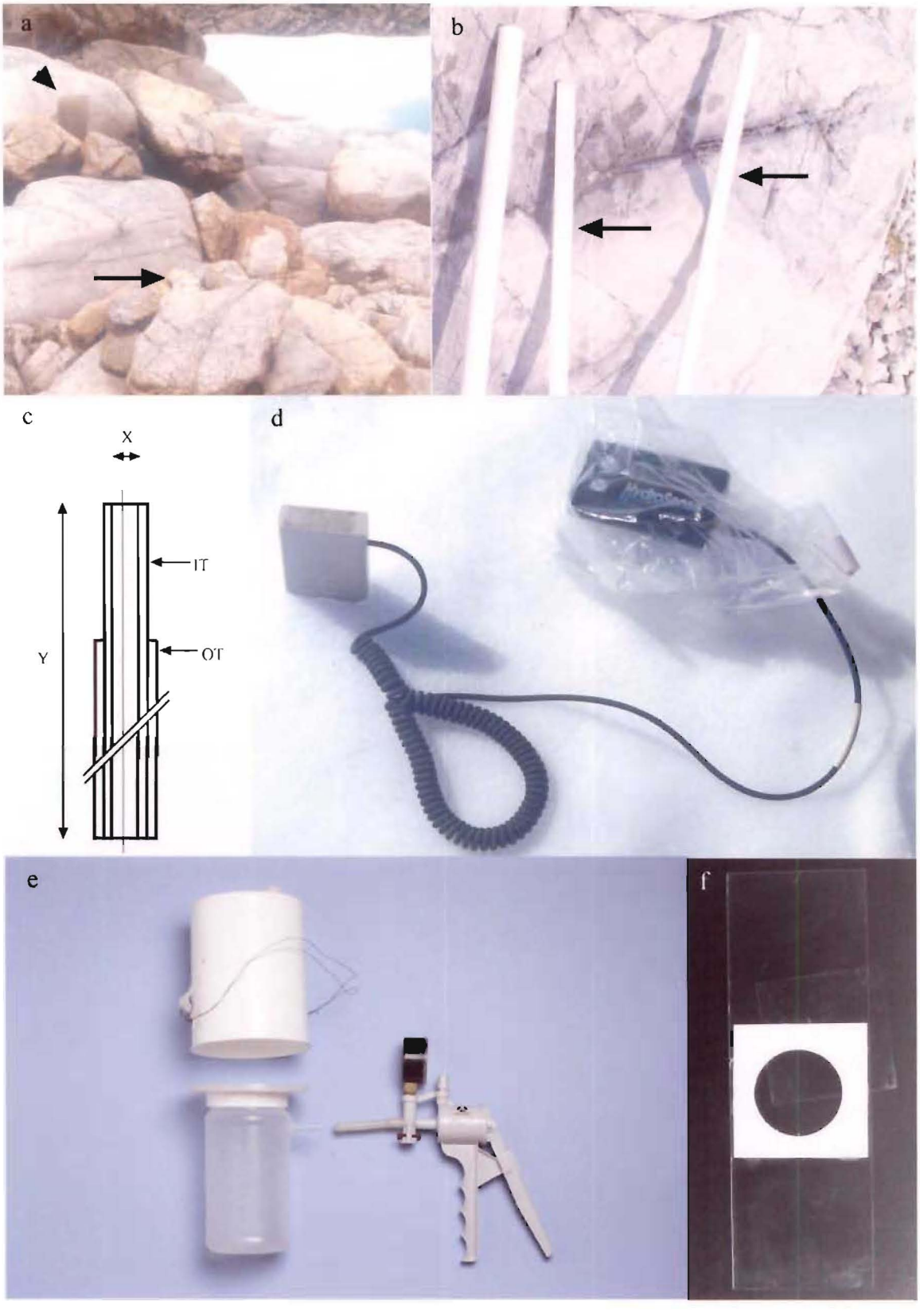


Fig. 4.2.2. a, light meter / data logger (arrow) and rain gauge (arrowhead), with tarn surface in background; b, photo of snow corer showing inner tube separated (arrows) and outer tube; c, diagram of corer showing inner tube (IT) and outer tube (OT), x=3 cm, y=1.3 m; d, TDR probe adapted for measuring snow LWC (black display box is approx. 15 cm long); e, apparatus for measuring elution of nutrients in spring snowmelt (see 4.2.8 and Fig. 4.2.4); f, manufactured chamber used for cell counting (slide is 25 mm wide).

(iv) The reactions were carried out in acid-cleaned 100 ml screw-top polyethylene containers.

Conductivity of the samples was measured with an RIAC CM100 conductivity meter. This was done to control for physical movement of ions in one snow type, in the absence of high enough Cl^- concentrations for detection using the method of Golterman and Clymo (1969).

Tests for interference were conducted using 1:1 mixtures of sample and standard. In all cases the measured concentrations compared well with theoretical concentrations (see Appendix 3).

Snow liquid water content (LWC). A Hydrosense probe (Fig. 4.2.2d), which uses Time Delay Reflectometry to measure the liquid water content of soil, was adapted for use in snow for the 1999 study period. The unit was hired from Scott Technical Instruments, Christchurch. Briefly, the unit works by sending an electronic signal through 2 probes inserted into the medium; the time delay between sending and receiving the signal describes a linear relationship with the liquid water content of the medium. This time delay (period number) was standardised for snow LWC by adding different known masses of water to known masses of snow in a container and recording the associated period numbers, resulting in a standard curve (Fig. 4.2.3). The R^2 value of 0.96 indicates the reliability of the technique for use in snow.

4.2.5. Snow algae sampling regime

A net made of nylon string and composed of 100 one metre squares was laid across an area of snow so that about half was laid on tarn snow, where algae had appeared in 1997-98 (see Chapter 2: study site), and half was on shore snow, which had not previously turned red (Fig. 4.2.1c, f, g). Corners of the grid were anchored by snow stakes with slots to prevent the cord detaching. Grid squares were numbered with engraved plastic tags wired to top corners of the squares, enabling random sampling of the area covered by the grid. Two areas were sampled: shore snow, which remained white all season, and tarn snow, which developed a red colour. An intermediate zone between the two areas was not sampled as it rapidly became inaccessible. On sampling days a random number table was used to select squares for sample removal. The grid was also used as an aid to monitor the patterns of snow breakup and melt and the distribution of red snow, using field sketches.

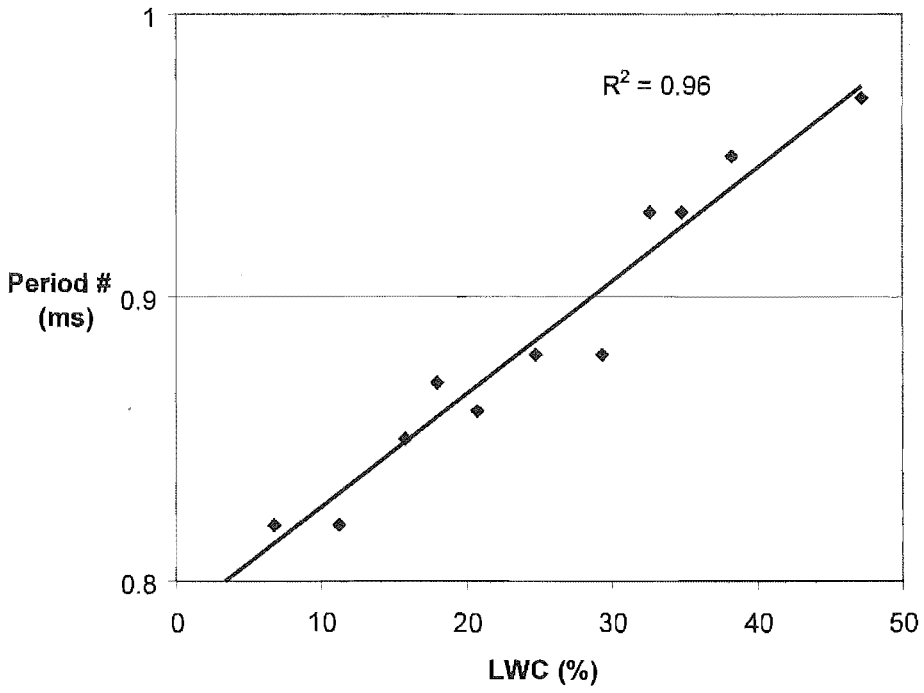


Fig. 4.2.3. Standard curve obtained for the Hydrosense TDR probe for Mt Philistine tarn snow during the 1999 study period. %LWC is obtained by weight of water added *100 / mass of dry snow. R^2 value at top right applies to trendline fitted in Microsoft Excel.

Modifications to the sampling regime during the 1999 study period were as follows.

(i) The grid was placed in a slightly different location on the tarn and shore surface, dictated by the smaller amount of snow in 1999 (Fig. 4.2.1d, f).

(ii) Records of snow breakup on the tarn surface were not made, because the sampling period was relatively short and changes were relatively insignificant over this time.

(iii) Snow cores for cell counts were taken at 4 a.m. on three occasions for comparison with daytime samples to investigate diurnal fluctuations in cell types and abundances.

(iv) Samples for cell counts were taken at 10 cm depth intervals up to 70 cm, from three replicate snow cores taken in an area of algal-coloured snow on 20 November, to investigate the distribution pattern of the tarn snow algae population with depth.

(v) Two replicate samples for cell counts were taken from the tarn water as close as possible to the snow edge on each sampling occasion.

4.2.6. Snow sampling methods

A snow corer (Fig. 4.2.1d, e) was used to take samples from randomly chosen squares from each of the two areas (snow on the tarn surface and snow on the shore). Six replicates per area on each sampling occasion were taken in 1998. Three depths (in the absence of coloured bands of snow at depth) were sampled for counting algae: 0-10, 30-40 and 60-70 cm. Two drops of Lugol's iodine solution, which was cooled in a snowbank, were quickly added to cell count samples, which were then stored away from heat and sunlight until transported to the laboratory.

Samples were taken for nutrient analysis in acid-washed polyethylene containers from the first three randomly selected squares of each snow area, usually on every second sampling occasion. Containers for DRP analysis of snow were also iodine-impregnated according to the method described by Mackereth *et al.* (1978). Samples were melted at low temperature in a snow cave and filtered using a Whatman GF/C glass fibre filter. Sample containers were washed with a small amount of filtrate before refilling, then stored in a snowcave. Samples for nutrient analysis were regularly carried down to Arthur's Pass village (within 1-4 days of collection) and stored in a freezer at -5°C.

Modifications to the sampling method for 1999 were as follows:

(i) Replication of the cell count samples was decreased from 6 to 4 randomly chosen squares in each sampling area.

(ii) The depths sampled were changed to 0-10 and 10-20 cm.

(iii) Replication of the samples for nutrient collection was increased from 3 to 4 randomly chosen squares in each sampling area, so that nutrient levels were available for all corresponding cell concentrations, increasing the power of statistical tests.

(iv) For each randomly chosen square, LWC of the surface snow at time of sampling was measured using the TDR probe (see 4.2.4).

(v) Samples for nutrient analysis were preserved at the site by adding 3 drops of 1 N HCl, reducing the pH in the samples to below 4. This reduced the logistical problem of freezing the samples, as the freezer in Arthur's Pass Village had become unavailable since the previous season. The samples were refrigerated, however, until transport back to the laboratory where they were frozen until analysis.

4.2.7. Cell counts

Some cell counts and observations were made at the study site using a Wild M11 field microscope, with a gas-powered lamp as the light source. Most samples were transported back to Christchurch at the end of the season for counting. A modified Palmer-Maloney counting chamber (Phycotech #168) of volume 0.0495 ml and depth 0.260 mm was used in 1998 because it was a good compromise for samples which contained very high to very low cell numbers. Samples were concentrated by sedimentation and removal of about 90% of the water using a Pasteur pipette, and then resuspending in the remainder. Weights of tubes dry, and before and after water removal were measured on an electronic balance to allow precise calculation of the concentration factor. The whole chamber was counted at 100X magnification (switching to 400X to distinguish between cells of uncertain classification) on an Olympus BH-2 microscope. Slides were counted until either 5 slides had been made for each sample or 100 cells of the dominant cell type had been counted.

Following a breakage of the original counting chamber, replacements were manufactured for the 1999 study period by attaching hole-punched squares of thin plastic to glass microscope slides with Loctite adhesive (Fig. 4.2.2f). Diameters of the holes were approximately 2 cm. The volume of each chamber was calculated using the following procedure. A micrometer gauge was used to measure the depth of the chamber (an average of the thickness of each corner of the plastic boundary + slide subtracted from the slide thickness in the middle of the chamber). Ten replicate measurements were then made by filling the chambers with water and recording the mass increase on an electronic balance sensitive to ±50 μg. Final volume used in calculations was an average of the volume calculated with the micrometer gauge and that calculated on the balance, for each counting chamber. These chambers were used in all cell counts following the 1999 summer season. The counting method used was the same as that in 1998 for all cells except *Chromulina* cf. *elegans*, which had such high cell densities that it was counted in ten random fields of view (or until 100 cells had been counted) on each slide.

All snow algae vegetative cells, cysts and dividing cells (to help interpret when population growth was occurring) were counted. Pollen and wind-dispersed algae, such as *Fischerella* sp.and cf. *Gloeocapsa* from surrounding habitats, were ignored (see Chapter 5 for consideration of these organisms).

4.2.8. Elution of nutrients from spring snow

Two dry snow samples were obtained from each of two sites: the headwaters of the Otira Valley on 21 September 1999, and the tarn study site on 28 September 1999 (on this date the tarn was a completely covered bowl of pristine snow). The first 20% of melt was obtained from each sample. A special invertible apparatus was used to do this (Fig. 4.2.2e). In the field, the apparatus, which was acid-washed in the laboratory, was rinsed with deionised water, which was kept and analysed for nutrient contamination. The apparatus was then cooled in the snow to prevent uncontrolled melting. A known mass of snow was added (Fig. 4.2.4a), followed by sufficient deionised water to raise the liquid water content of the sample to 20% (Fig. 4.2.4b). The container was rotated so the deionised water was repeatedly passed through the snow crystals, until the water content had reached 40% (measured with the TDR probe, Fig. 4.2.4d). The lid was then placed on the container, the apparatus was turned upside down so the GF/C filter was beneath the snow, the plug was opened and the interstitial water was removed into the lower container by applying suction with a hand-operated pump (Fig. 4.2.4f). The sample was then treated as the other snow samples for nutrient analysis (see section 4.2.6(v)). A bulk snow sample was collected on each occasion for comparison.

A melt fraction of 20% was chosen from previous work (e.g. Cadle and Dasch 1984, Davis 1991) in which a large quantity of the total ions were eluted in the first 20% of melt. The method is shown diagrammatically in Fig. 4.2.4. The whole process took approximately 1.5 hours for each replicate.

4.2.9. Statistical analyses

Means of cell count and nutrient analysis results were analysed for significant differences using analysis of variance (Anova) on the statistical computing package S-Plus 2000 (Mathsoft 1999). Homogeneity of variance was assessed by fitting the Anova models and then plotting fitted values against residuals and visually inspecting the graph. Where necessary, data were log-transformed to achieve homogeneous variance. Where significance ($P<0.05$) was present between values from tarn and shore snow, the cause of this significance was assessed using Tukey tests. Comparisons of cell type abundances within single days in tarn snow were made using paired 2-sample t-Tests (Mathsoft 1999).

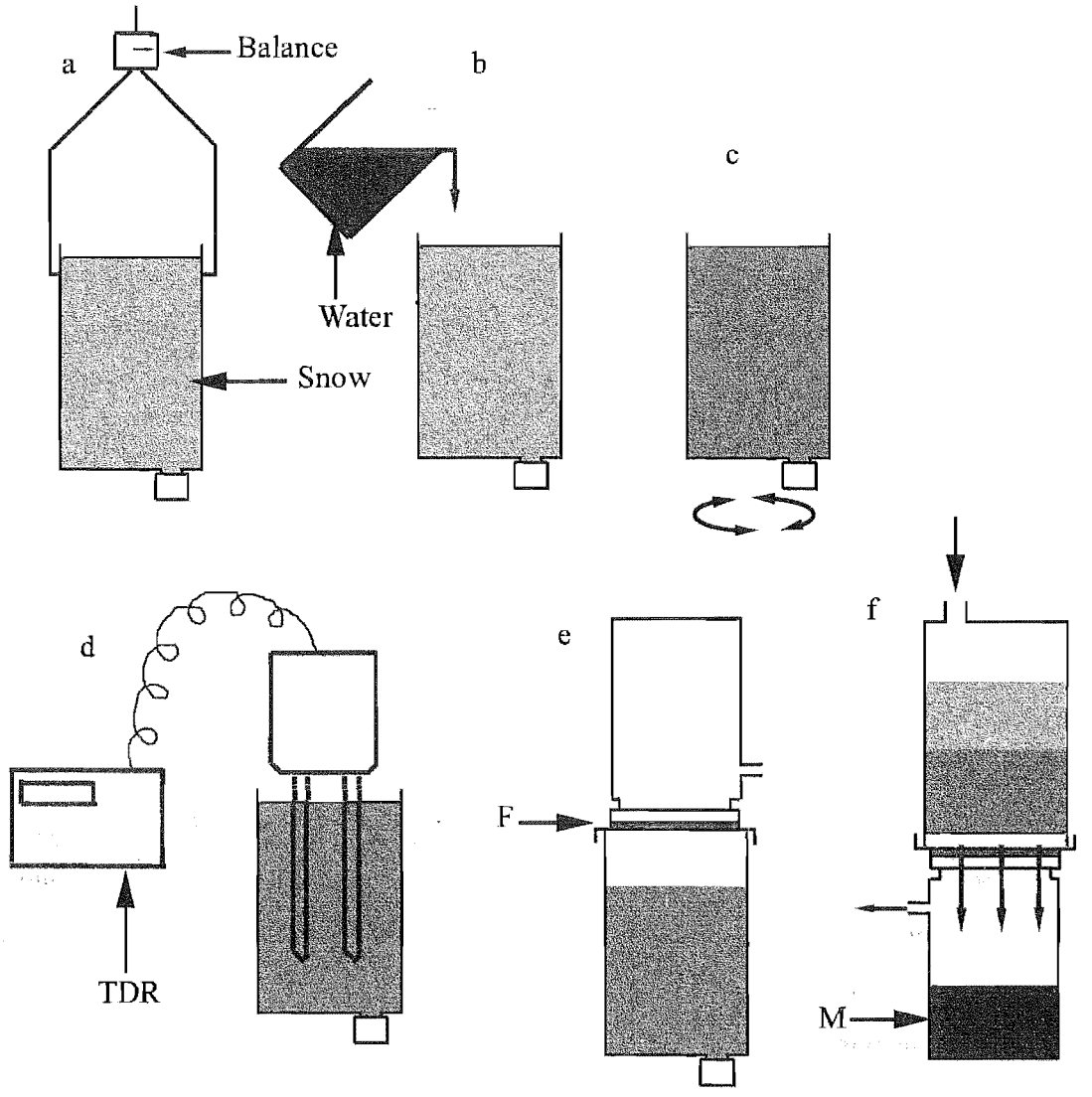


Fig. 4.2.4. Elution of nutrients from spring snow: summary of method. a, snow sample placed in container and weighed; b, known mass of water introduced to snow sample to initiate melting; c, rotation of container by hand to continually pass water over the snow crystals to melt the sample; d, monitoring with TDR probe until desired water content of 40% (20% melt + 20% added water) is reached; e, top with filter (F) attached; f, interstitial meltwater for analysis drawn out of snow sample under suction with unit inverted and plug removed (top arrow).

4.2.10. Field safety precautions

Work on the unstable tarn snow was safeguarded using a harness, rope and self-belay device. The rope was anchored using two equalised vertically placed snow stakes. A helmet and emergency locator beacon (H.E.L.P. Mark 1, manufactured by Frank Millar &Co. Ltd, Christchurch) were worn at all times away from the campsite (Fig. 4.2.1d). A mountain radio (hired from Canterbury Mountain Radio Service) was used for weather forecasts every evening when reception was obtainable.

4.3. Results

4.3.1. Weather record.

Table 4.3.1 shows the qualitative weather record during the 1998 study period. Two major snow events occurred: a small one on day 26 from the south (5 cm in the top basin, not detectable at the tarn site), and a large one from day 37-39 from the northwest (over 40 cm in the top basin, 39 cm at the tarn site). Seven fine periods occurred of 1-7 days in length, separated by precipitation events lasting for 1-6 days. Generally, sampling days and habitation of the site (rather than Arthur's Pass Village) were dictated by weather and consequent safety considerations, although two major storms were weathered on site (days 26 and 29-32).

Table 4.3.2. shows the qualitative weather record for the 1999 study period. Rain was frequent and often heavy during days 1 to 13. The snow sampling period began on day 7 during two days with no rain and included the subsequent storm conditions, during which strong north-westerly winds predominated. Over 240 mm of rain fell during this storm (Fig. 4.3.1). The north-west storm was followed (as is typical) by a storm from the south bringing a small amount of snow. The second half of the sampling period was made during mostly fine weather. Thus, all types of weather conditions were included.

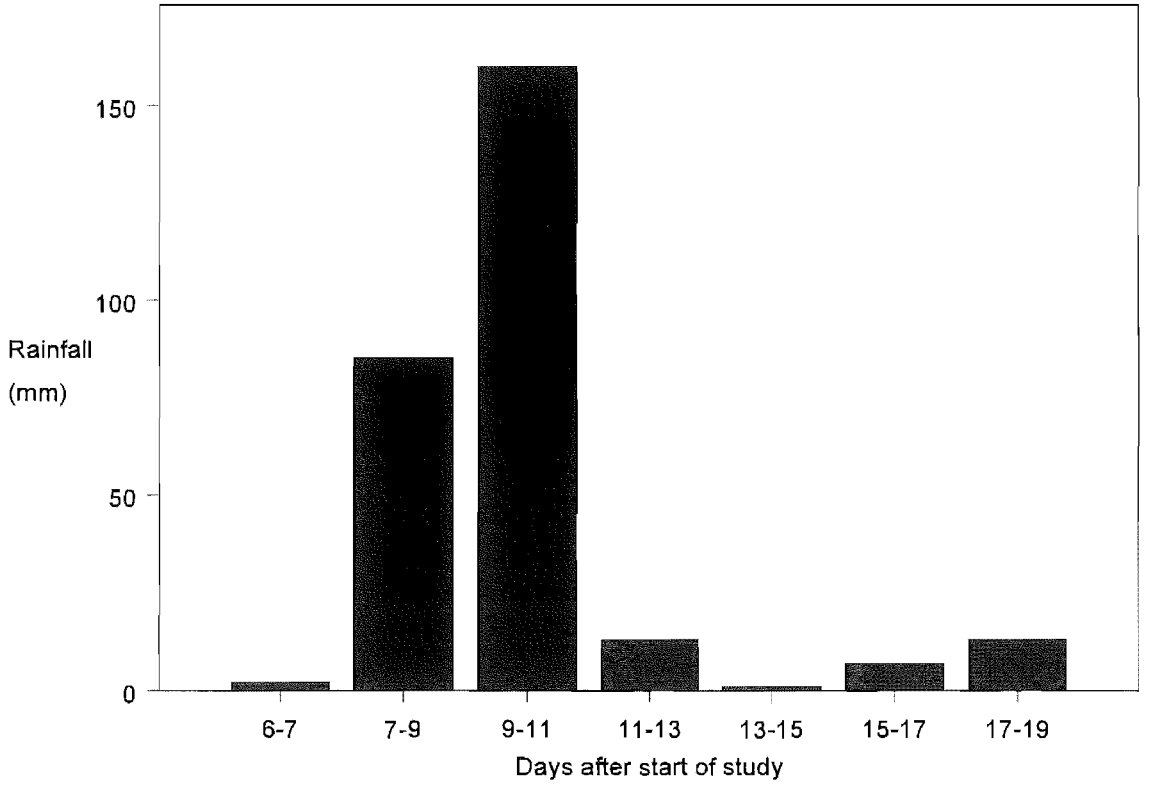


Fig. 4.3.1. Rainfall during the 1999 snow algae study period.

Table 4.3.1. Qualitative weather data and sampling schedule, 1998 study period.

Date	Day of Study	Weather Conditions					Samples taken	
		Fine[1]	Cloudy[2]	Rain[3]	Snow[3]	Unknown	Cell count	Nutrient analysis
1/11/98	1	+	+				+	
2	2					+		
3	3					+		
4	4					+		
5	5					+		
6	6					+		
7	7					+		
8	8					+		
9	9					+		
10	10					+		
11	11					+		
12	12	+						
13	13	+	+					
14	14	+					+	
15	15	+						
16	16	+						
17	17	+					+	
18	18	+	+					
19	19	+					+	
20	20		+	+				
21	21		+	+				
22	22		+	+				
23	23		+					
24	24	+					+	+
25	25	+	+					
26	26				+			
27	27	+					+	
28	28	+						
29	29	+	+					
30	30		+	+			+	+
1/12	31		+	+				
2	32	+	+					
3	33	+					+	
4	34	+	+					
5	35		+	+				
6	36		+	+				
7	37				+			
8	38				+			
9	39				+			
10	40		+	+				
11	41	+	+					
12	42		+	+				
13	43		+	+				
14	44	+	+				+	+
15	45	+	+					
16	46	+						
17	47	+					+	+
18	48		+	+				
19	49		+	+				
20	50		+	+				
21	51		+	+				
22	52		+	+				
23	53		+	+				
24	54	+					+	+
25	55	+						
26	56	+						
27	57	+					+	
28	58	+	+					
29	59		+	+				
30	60		+	+				
31	61		+	+				
1/1/99	62	+	+					+
2	63	+						
3	64	+						
4	65	+						

[1] "Fine" refers to periods of full sunlight without significant cloud cover.

[2] "Cloudy" refers to periods of continuous cloud cover. Many days without rain included interspersed fine and cloudy periods.

[3] "Rain" and "snow" refers to any precipitation during the day. Usually rainfall was continuous and heavy when it occurred.

Table 4.3.2. Qualitative weather and sampling schedule, 1999 study period.

Date	Day of Study	Weather conditions				Samples collected			
		Fine[1]	Cloudy[2]	Rain[3]	Snow[3]	Cell count	4a.m. cell count	Nutrient analysis	Fris-bee[4]
8/11/99	1		+	+					
9	2		+	+					
10	3		+	+					
11	4		+	+					
12	5				+				
13	6		+						+
14	7		+			+		+	
15	8		+	+			+		
16	9		+	+		+		+	
17	10		+	+	+				
18	11		+			+		+	
19	12		+	+					
20	13		+		+	+		+	
21	14		+				+		
22	15	+				+		+	
23	16	+					+		
24	17		+	+		+		+	
25	18	+							
26	19	+	+			+		+	+
27	20				+				
28	21		+						
29	22	+							
30	23	+							
1/12	24		+						
2	25		+						
3	26		+	+					
4	27		+						
5	28		+	+					
6	29		+	+					
7	30	+							
8	31	+							
9	32	+							+
10	33	+							

[1], [2], [3] See Table 4.3.1.

[4] Samples taken from Frisbee aerobiota collectors during the snow algae study period (see Chapter 5: Dispersal for other dates).

4.3.2. Light intensity

Photon flux was greatly magnified in the surface snow when compared to the incident light intensity (Table 4.3.3). Therefore, even during cloudy days without rain the algae were exposed to light levels greater than incident full sunlight (approx. 2000 μmol m^{-2} s^{-1}). This effect was the same in both white and red snow.

Maximum light intensities during the major storm in 1999 dropped to less than 20% of their fine weather values (Fig. 4.3.2). The influence of cloud cover caused incident light to fluctuate considerably even during fine weather.

Table 4.3.3. Selected photon flux measurements taken at the tarn site during the 1998 study period.

Date	Weather conditions		Red snow		White snow	
	Fine	Cloud	Incident[1] photon flux[3]	Total[2] photon flux[3]	Incident[1] photon flux[3]	Total[2] photon flux[3]
15/11/98	+		2210	5560	2050	5020
25	+	+	637	1730	774	2540
28	+		2850	5620	2390	4930
3/12	+		2550	5600	2490	5520
12	+	+	1690	3970	2000	5010
15	+	+	NA	NA	1720	3960
26	+		2230	3680	2330	5230

[1] Spherical light sensor placed on black non-reflective material at snow surface.
[2] Spherical light sensor placed on snow surface.
[3] Measured between 11:45 a.m. and 1 p.m. (μmol m^{-2} s^{-1}).

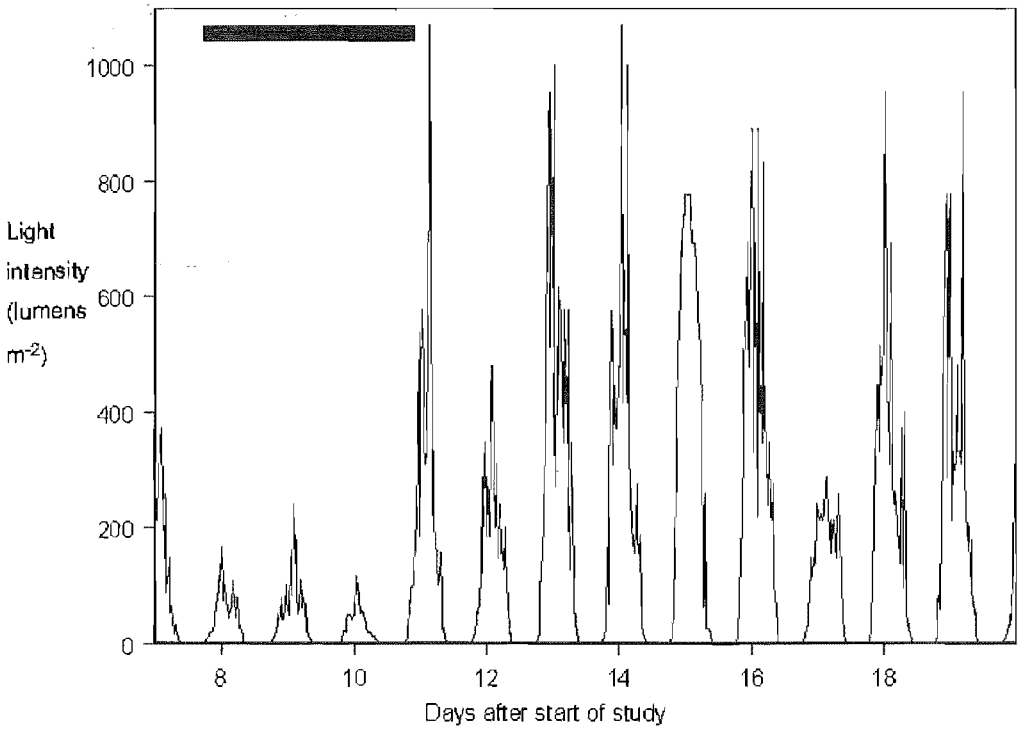


Fig. 4.3.2. Light intensities during the 1999 snow algae study period. Thick bar above days 7-11 indicates period of greatest rainfall (see Fig. 4.3.1). Multiple peaks on each day reflect intermittent cloud cover during fine weather, typical of Westland mountains. Day 15, with only one major peak, was an unusual day with no cloud cover.

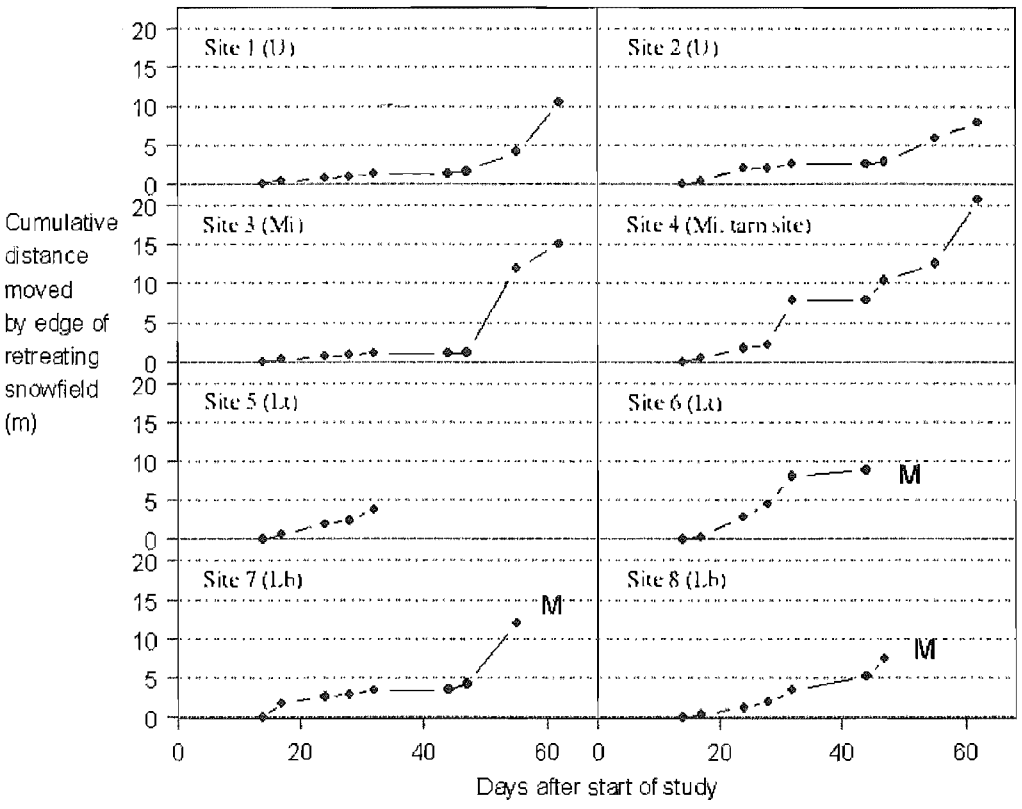


Fig. 4.3.3. Retreat of eight snowfield edges on Mt Philistine, 1998 study period. For precise site locations, refer to map (Fig. 2.1). The site 5 marker was lost after day 32. M indicates complete melting of the snowfield, U=upper basin, Mi=middle basin, Lt=top of lower basin, Lb=bottom of lower basin.

4.3.3. Snow melt

The time of fastest snowfield area retreat varied between sites in different basins (Fig. 4.3.3). Rapid snowfield disappearance resulted when gradual melting had produced a shallow layer of snow over a low-angle rock slope. All persistent snowfields were located in deeper shaded hollows where rocks extending beneath the snow were subject to little solar warming.

Melt of snow at the tarn site was strongly influenced by precipitation, which caused the level of water in the tarn to rise and cover the snow, and then subside gradually during fine weather (Fig. 4.3.4). On day 24, after 3 days of heavy rain, there was still some water covering the snow in the centre of the tarn. The large snowfall that occurred between days 37 and 39 covered the entire tarn surface, but gaps quickly reopened (day 44). The smaller snowfall which occurred on day 26 had little effect on the pattern of snow on the tarn and quickly melted.

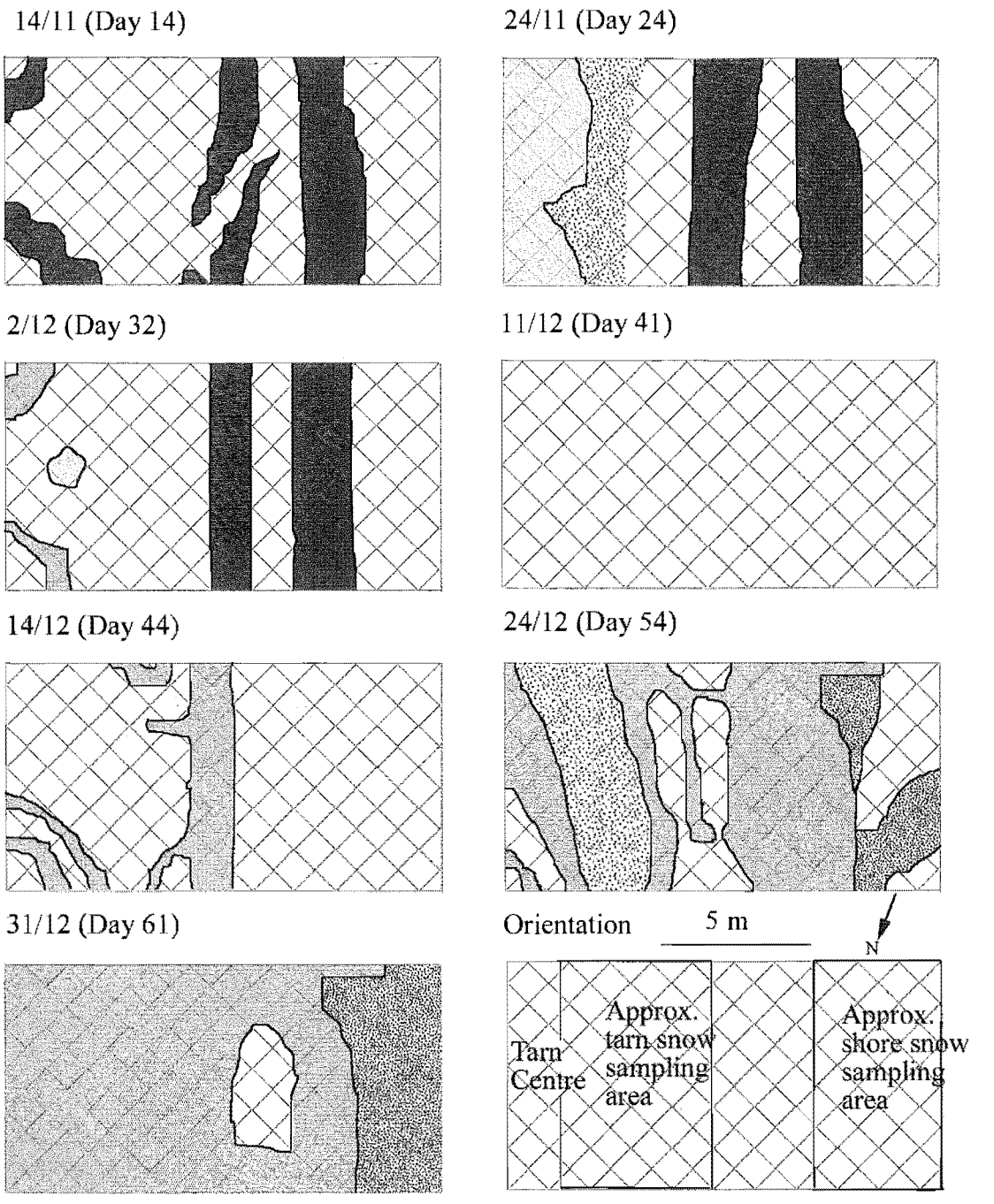


Fig. 4.3.4. Diagrams showing breakup of snow beneath the sample area during Nov.-Dec. 1998. The grid of connected squares represents the actual grid used for random sampling. The positions shown for the tarn and shore snow sample area are marked as approximate because they varied with the location of accessible snow. Sometimes, although coloured snow was present, it was visible only when the surface of the snow was disturbed (e.g. Days 32 and 44), and in this case its distribution could not be ascertained.

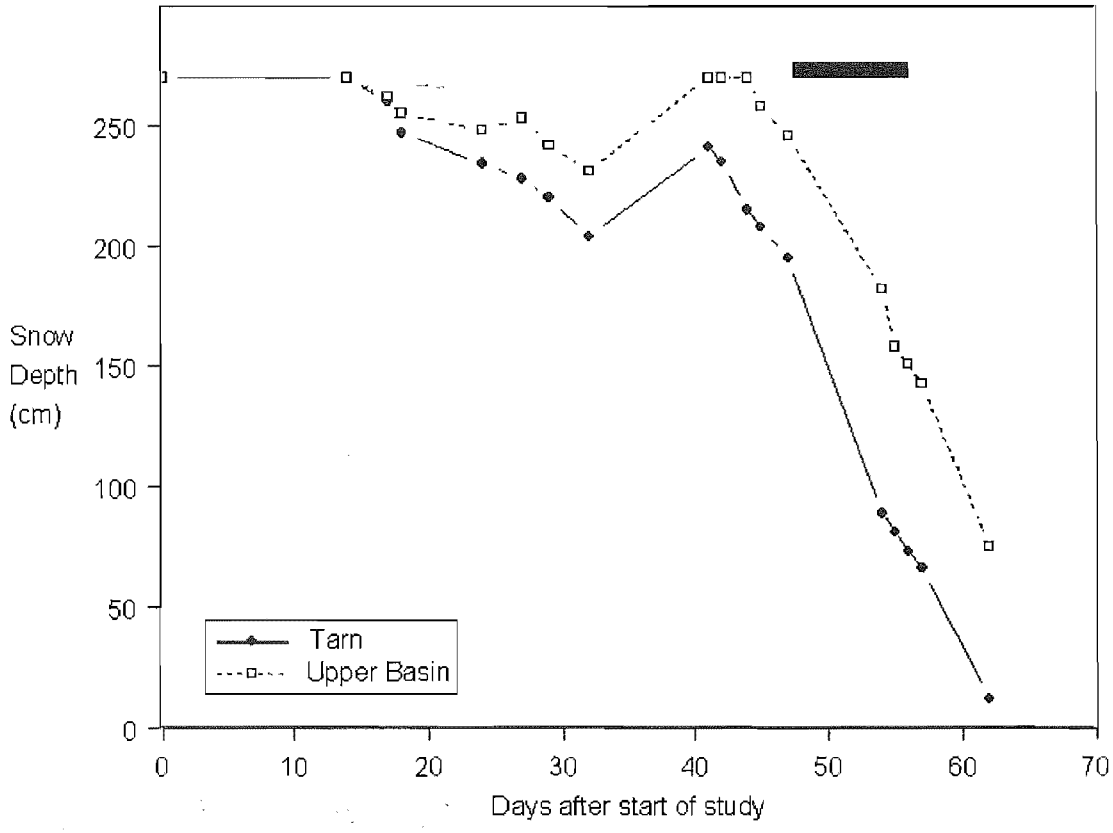


Fig. 4.3.5. Snow depth at two sites on Mt Philistine during 1998 study period. Measurements were taken from one graduated snow stake at each site driven to the bottom of the snowpack. Tarn measurements refer to a snowpack resting on bedrock immediately adjacent to the tarn snow. Thick bar at top of graph indicates period of sustained north-westerly rain. Tarn site corresponds to site 3 in Fig. 4.3.3.

Periods of marked decrease in snow depth during the 1998 study occurred from day 15-32 and day 41 onwards (Fig. 4.3.5). Both higher and lower sites followed similar temporal patterns of decrease, although snowmelt was faster at the lower site and effect of snowfalls was greater at the higher site. The large snowfall (days 37-39, Table 4.3.1) restored the snowpack to nearly day 0 depth. The earlier snow event measurably affected snow depth at the top basin site but not the tarn site. North-west rain prevailed during the greatest rate of snow depth loss (15.1 cm d^{-1}, days 47-54).

The maximum rate of snow depth loss during the 1999 study period (Fig. 4.3.6) was 6.5 cm d^{-1}. This rate was also sustained for the shorter time of four days. However, the maximum rate once again occurred during rain and north-westerly winds.

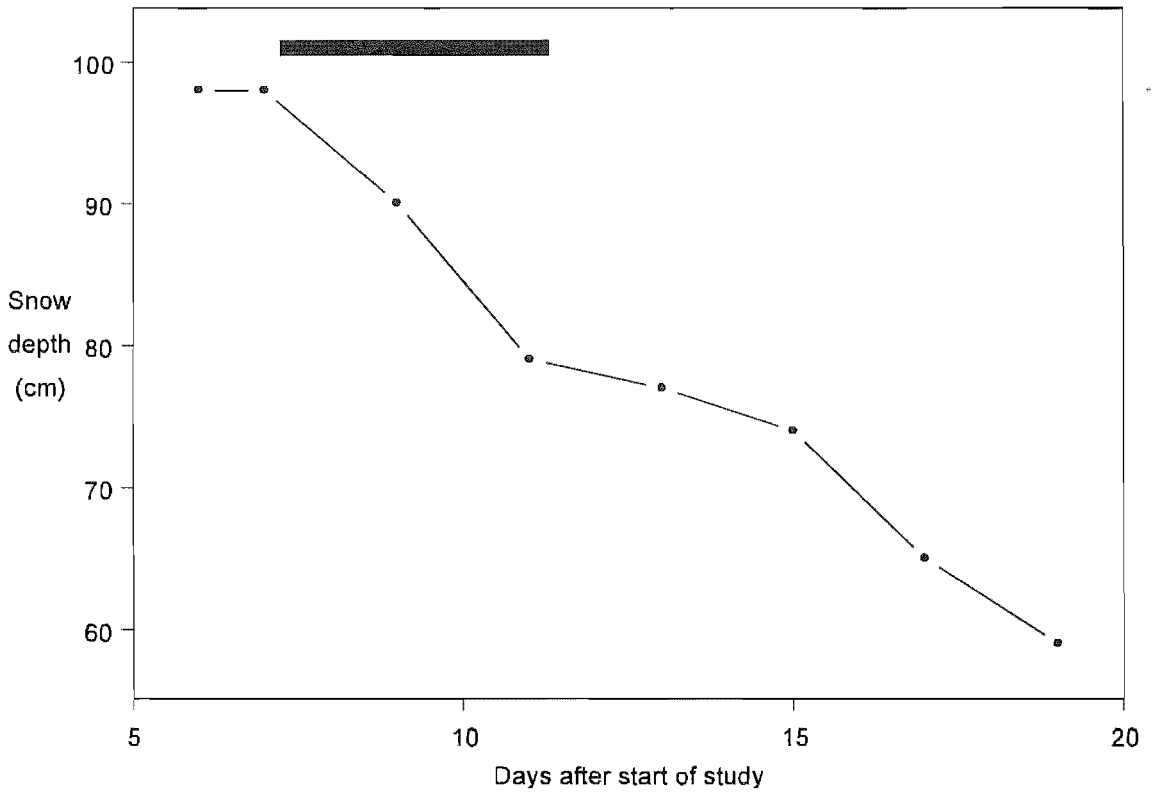


Fig. 4.3.6. Snow depth at the tarn site on Mt Philistine during 1999 study period. Measurements refer to a snowpack resting on bedrock immediately adjacent to the tarn snow. Thick bar at top of graph indicates period of sustained north-westerly rain. Tarn site corresponds to site 3 in Fig. 4.3.3.

4.3.4. Nutrient concentrations in snow at tarn site

NH_4-N in tarn and shore surface snow was similar during the 1998 study period, except on day 54, when tarn snow concentrations were significantly lower (Fig. 4.3.7). Concentrations in tarn and shore snow were similar throughout the 1999 study period (Fig. 4.3.8). The mean concentration of 21 μg NH_4-N l^{-1} recorded over all samples in 1999 was significantly higher (t-Test, P=0.0013) than the mean of 4.2 μg l^{-1} recorded in 1998.

NO_3-N concentrations were similar in both tarn and shore snow throughout the 1998 study period (Fig. 4.3.9), and were lower than NH_4-N concentrations. The NO_3-N concentration in both snow types was seldom detectable in 1999 samples. Values up to 5 μg l^{-1} were recorded in 5 individual samples, but no pattern was evident (data not shown).

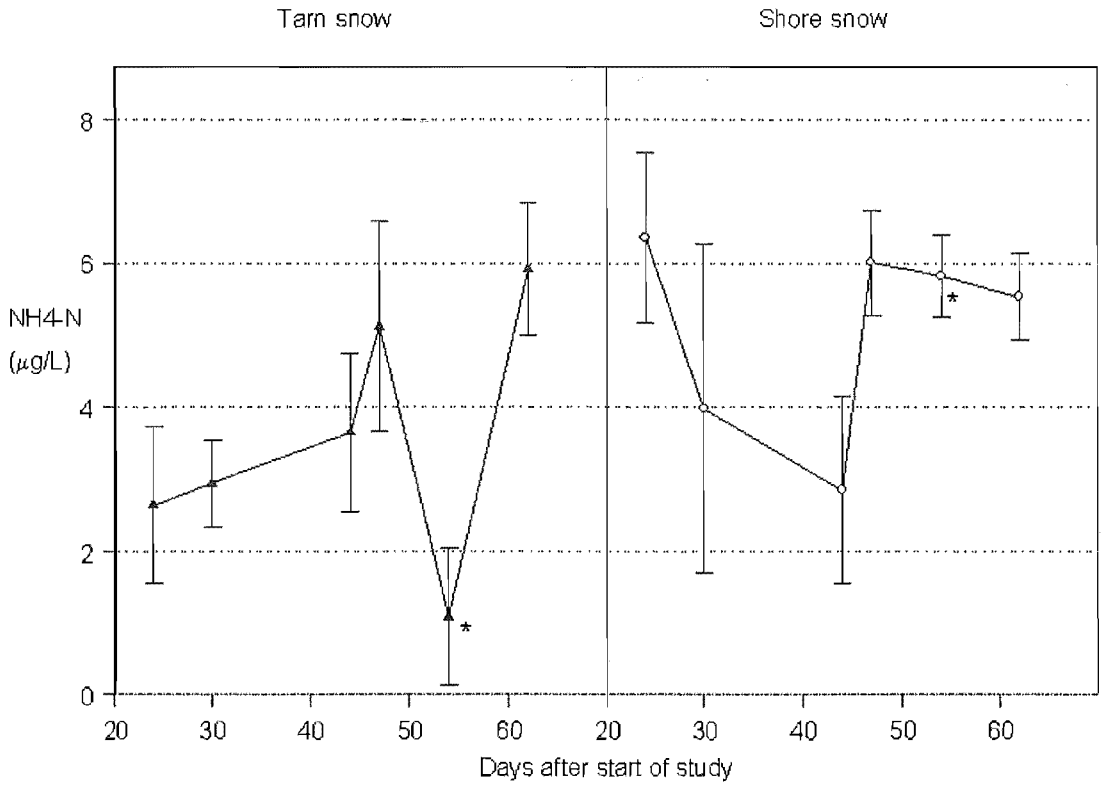


Fig. 4.3.7. NH_4-N concentrations in tarn and shore bulk surface snow, 1998 study period. Error bars represent ±1 SE. Data are means of 2-3 replicate samples from each snow area. Day on which NH_4-N concentration was significantly lower in tarn snow than in shore snow (Tukey test, $P<0.05$) is denoted by *.

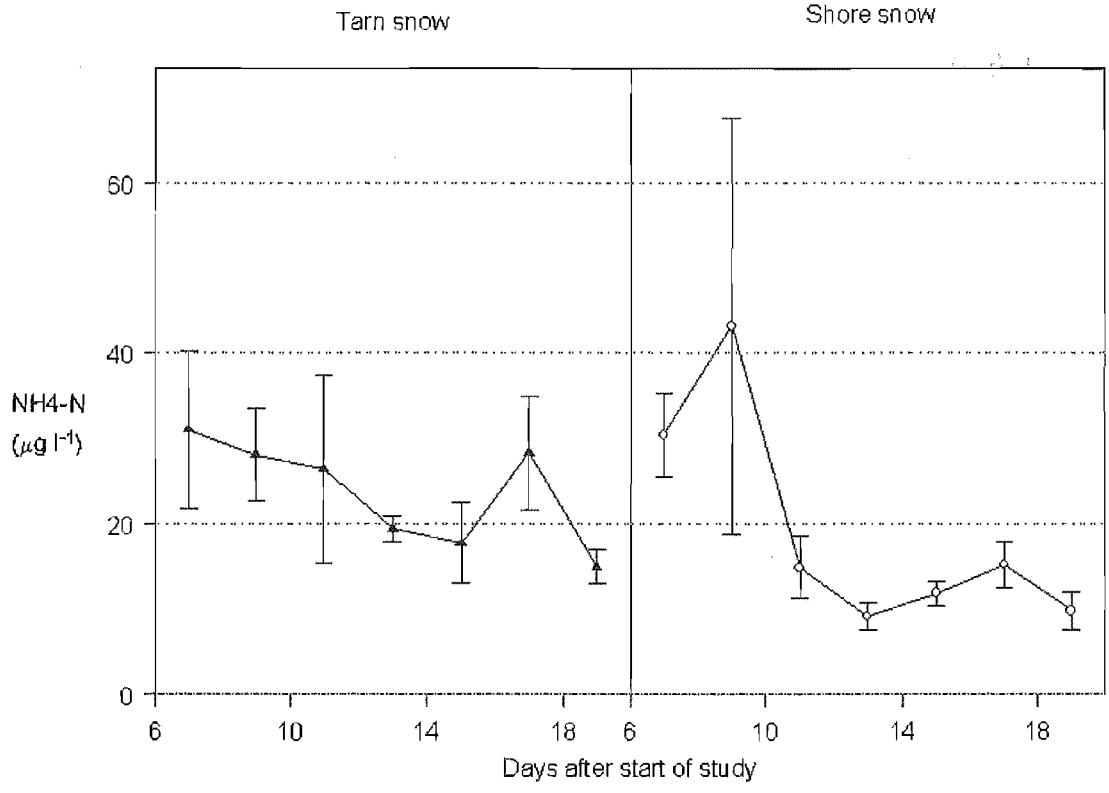


Fig. 4.3.8. NH_4-N concentrations in tarn and shore bulk surface snow, 1999 study period. Error bars represent ±1 SE. Data are means of 4 replicate samples from each snow area.

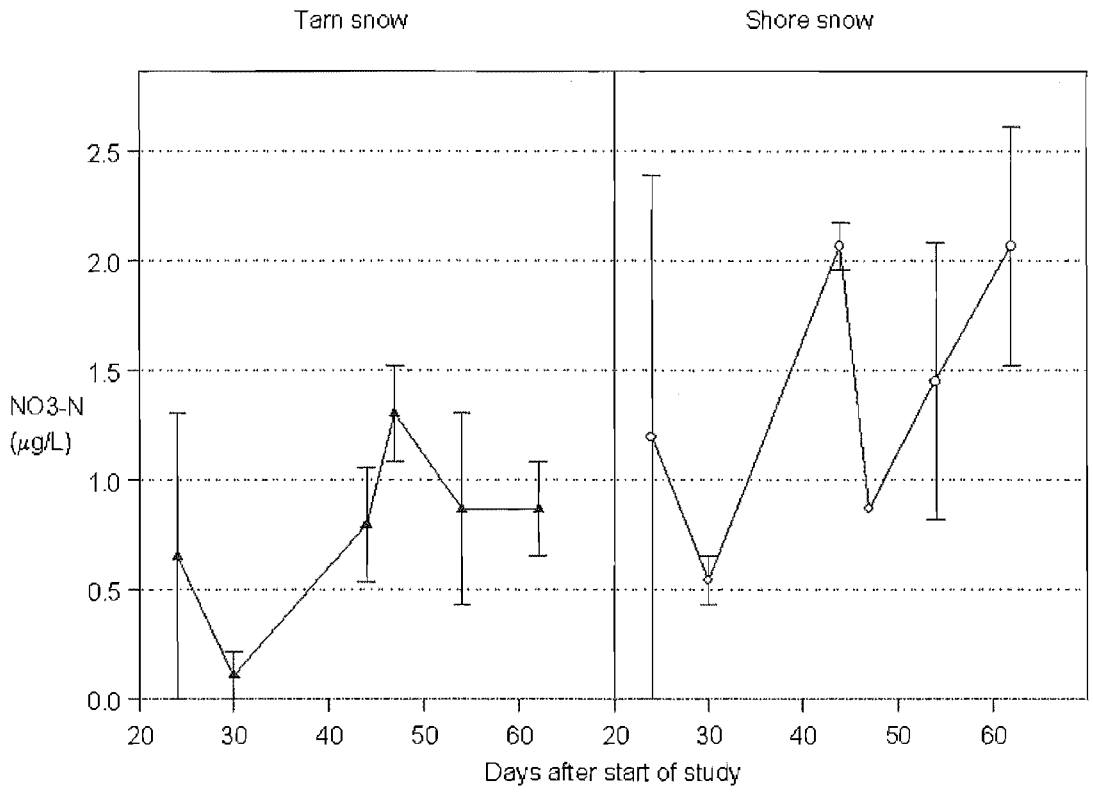


Fig. 4.3.9. NO_3-N concentrations in tarn and shore bulk surface snow, 1998 study period. Error bars represent ±1 SE. Data are means of 2-3 replicate samples from each snow area.

DRP concentrations were similar between tarn and shore snow at all times during the 1998 study period (Fig. 4.3.10), but were significantly higher in both snow types on day 47 than on day 24. During the 1999 study period (Fig. 4.3.11) DRP was significantly higher in shore snow on day 15 than in tarn snow, and mean concentrations from both snow types were significantly higher on day 17 than on other days (Tukey test, $P<0.05$). The mean concentration of 6.5 µg DRP l^{-1} over all samples in 1999 was significantly higher than the mean concentration of 1.7 µg l^{-1} recorded in 1998 (t-Tests, $P<0.05$).

Conductivity in tarn and shore snow during the 1998 study period was almost identical (Fig. 4.3.12), but was significantly greater on day 44 in both snow types than on days 30 and 54 (Tukey test, $P<0.05$).

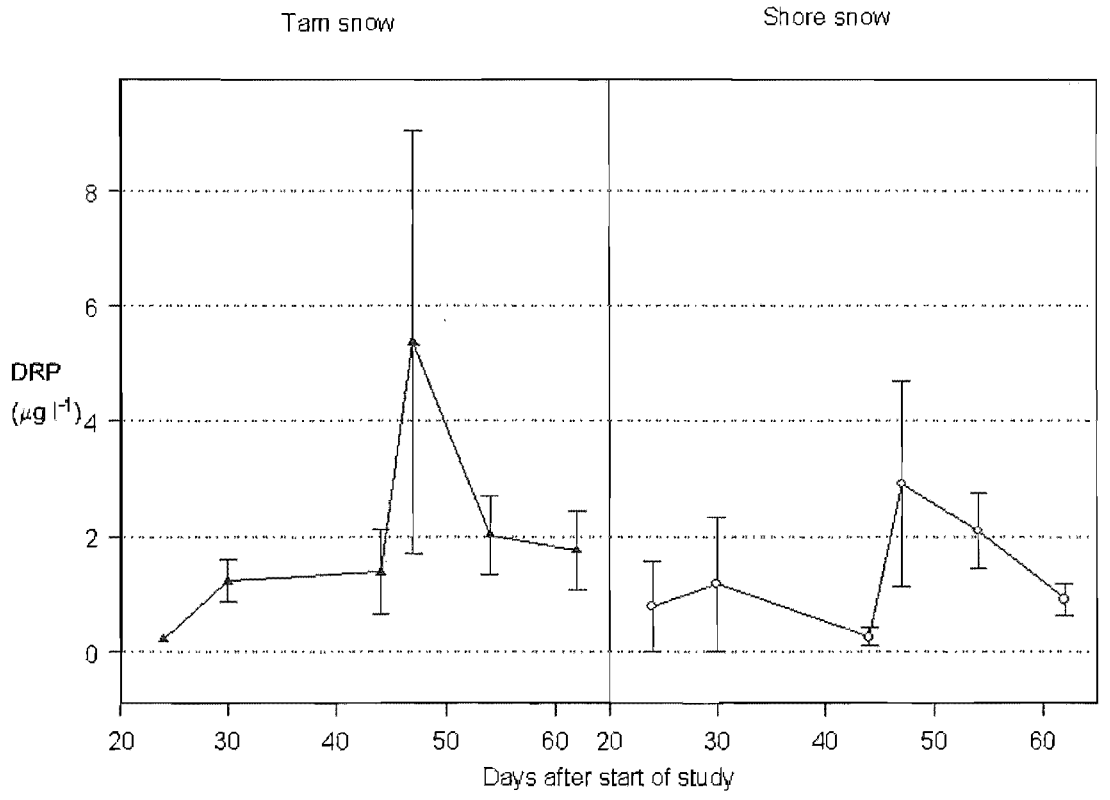


Fig. 4.3.10. DRP concentrations in tarn and shore bulk surface snow, 1998 study period. Error bars represent ±1 SE. Data are means of 2-3 replicate samples from each snow area.

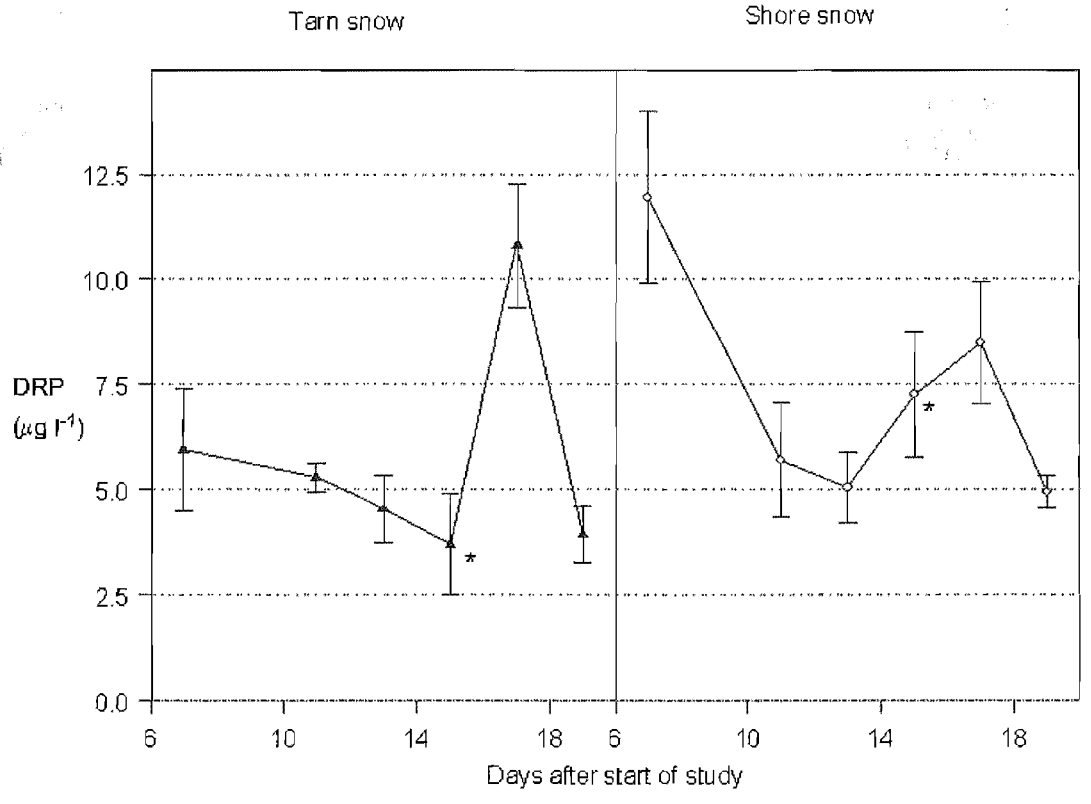


Fig. 4.3.11. DRP concentrations in tarn and shore bulk surface snow, 1999 study period. Error bars represent ±1 SE. Data are means of 4 replicate samples from each snow area. Day on which DRP concentration was significantly lower in tarn snow than in shore snow (Tukey test, $P<0.05$) is denoted by *.

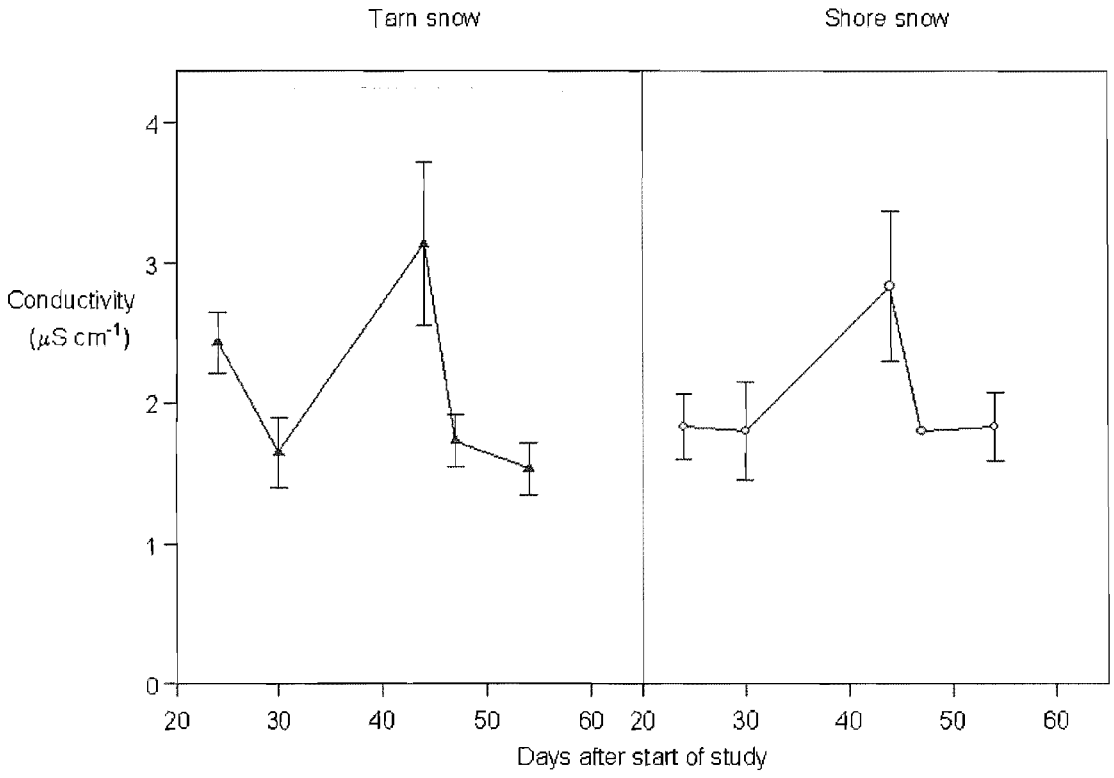


Fig. 4.3.12. Conductivity of tarn and shore bulk surface snow, 1998 study period. Error bars represent ±1 SE. Data are means of 1-3 replicate samples from each snow area.

4.3.5. Elution of nutrients from spring snow

The fraction of snowmelt eluted from bulk samples contained greater concentrations of nutrients than bulk snow samples in all cases (Table 4.3.4, "concentration factor"). NH_4-N displayed the greatest concentration effect in initial elution of the three nutrients tested. There was some NH_4-N contamination of the apparatus in both experiments (Table 4.3.4, "pre-rinse"), but this was insufficient to account for the observed concentration effect.

4.3.6. Liquid water content (LWC) of snow

LWC of shore snow remained at 7-9% throughout the 1999 study period (Fig. 4.3.13). Tarn snow LWC reached a maximum of 28.4±11.6% by weight, which was significantly higher than shore snow LWC (Anova, day:site P=0.033). However, because there was no detectable variation amongst shore snow replicates on most days, variances could not be made homogeneous. The increase in LWC of tarn snow corresponded to the period in which heavy rain occurred (Fig. 4.3.1).

Table 4.3.4. Concentration of nutrients in initial melt fractions from spring snow samples, Otira Valley and Mt Philistine.

Site	Solution	Nutrient concentrations ($\mu g\ l^{-1}$)		
		NH_4-N	NO_3-N	DRP
Otira Valley	Pre-rinse[1]	2.8	NA	0
	Bulk snow	7.2	1.8	5.3
	Eluted melt[2]	21.4± 4.9	3.2±1.3	4.9±0.5
	Eluted melt adjusted for dilution[2]	63.7±14.5	9.4±3.7	14.5±1.3
	Concentration factor[2]	8.8± 2.0	5.2±2.1	2.8±0.3
Mt Philistine tarn snow	Pre-rinse	5.0	NA	0
	Bulk snow	12.8	0	3.3
	Eluted melt[2]	27.4± 7.4	1.7±0.8	4.7
	Eluted melt adjusted for dilution[2]	49.1±13.3	2.9±1.3	8.5
	Concentration factor[2]	3.9± 1.1	1.9±0.9	2.5

[1] Concentration of nutrients in solution collected from washing of apparatus in deionised water.
[2] Data are means of two replicates ± SE (except DRP in Mt Philistine experiment, unreplicated); NA = not analysed.

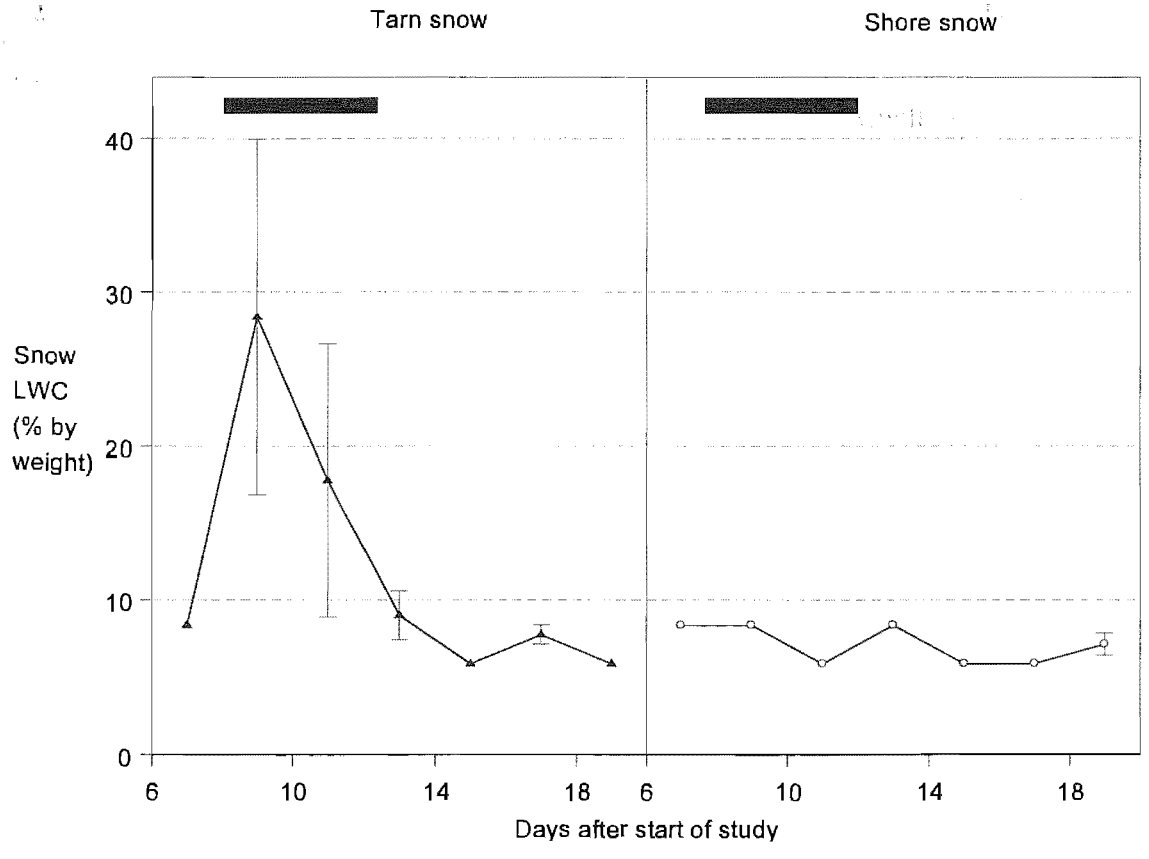


Fig. 4.3.13. LWC of snow by weight measured with Hyrosense probe in tarn and shore surface snow during 1999 study period. Data are means of 4 replicates in each snow type. Error bars represent ±1 SE. Thick bar at top of graph indicates period of heavy rain.

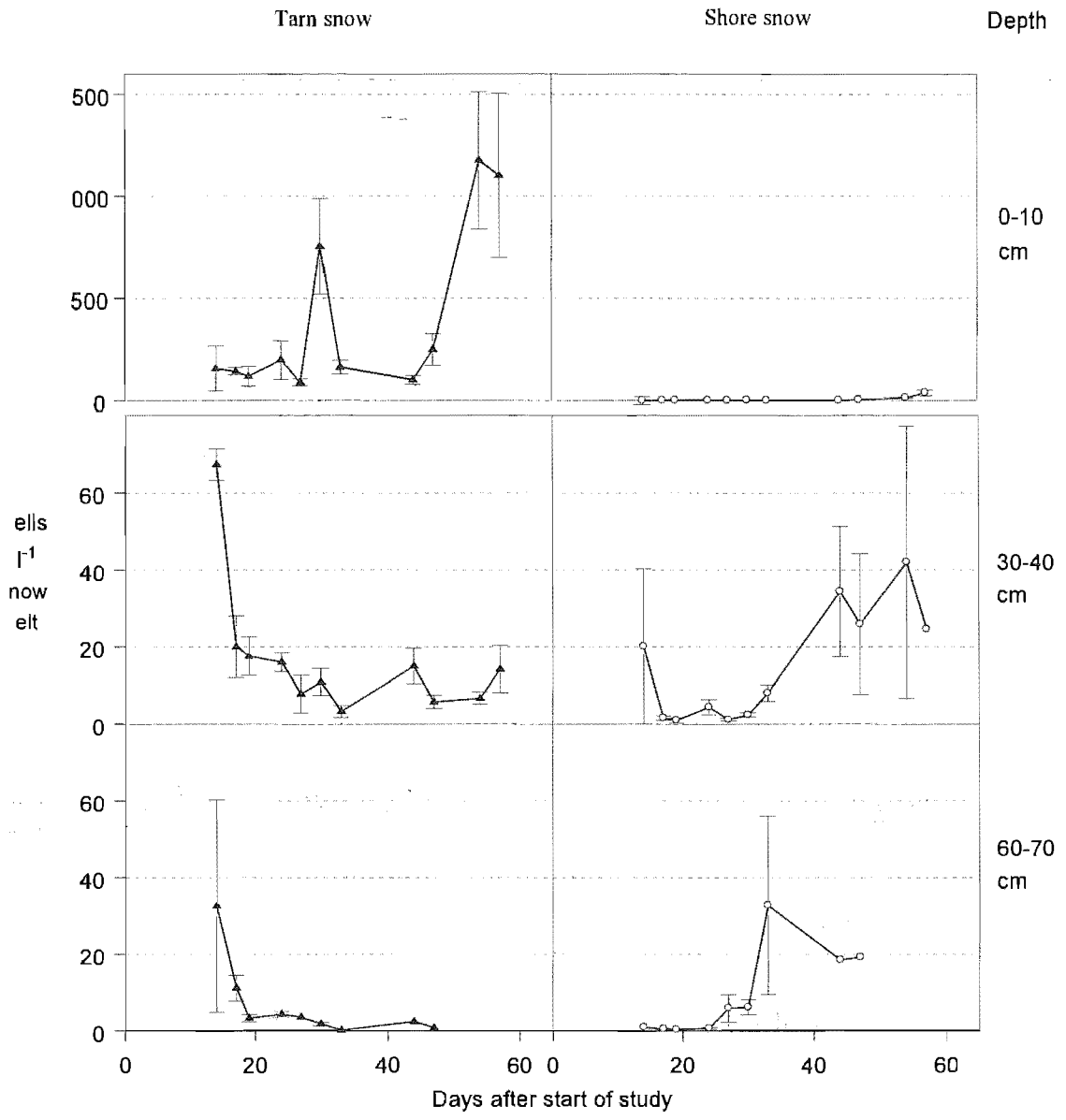


Fig. 4.3.14. Mean total abundance of snow algae at the three sample depths from 1998 snow cores. Means are of up to 6 cores from each sample area. Error bars represent ±1 SE. Note different vertical scale for 0-10 cm depth.

4.3.7. Snow algae cell numbers and distributions

Cells in tarn snow reached much greater abundance than in shore snow during the 1998 study period (Fig. 4.3.14). The cell concentration peak in tarn snow on day 54 was significantly greater than concentrations between day 0-27 and 33-47, when they remained low (Tukey test, $P<0.05$). The cell abundance peak on day 30 was significantly greater than abundances on days 0 and 27. Cells were apparently lost from the surface snow following the first peak. Snow was visibly coloured first on day 24 (Fig. 4.3.4), corresponding to a concentration of about 200 cells ml^{-1}. At greater

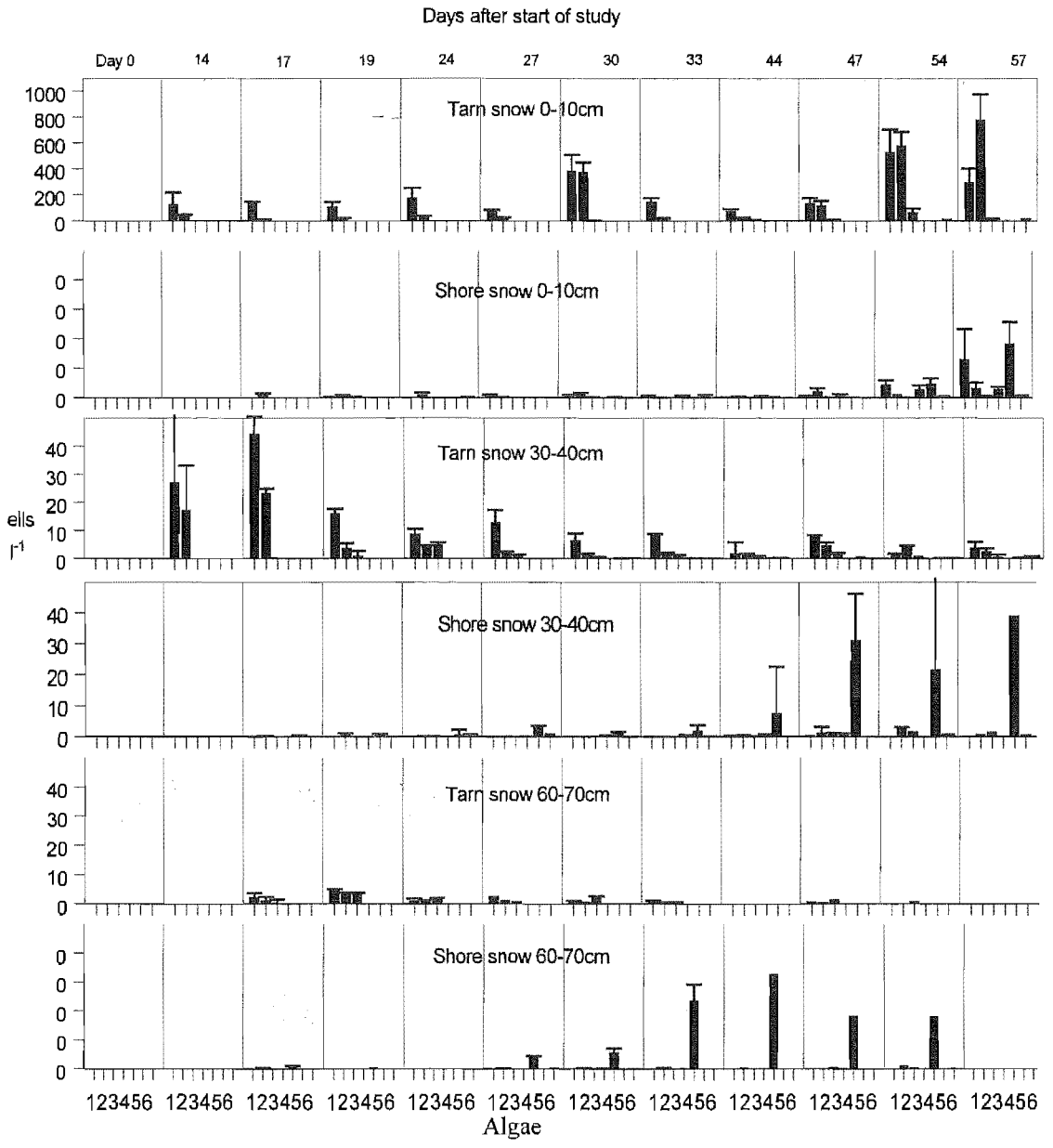


Fig. 4.3.15. Cell numbers of six different cell types in tarn and shore snow at three depth ranges sampled during 1998 study period. Data are means of up to six replicate cell counts. Error bars represent ±1 SE. Concentrations refer to melted snow samples. Key to "Algae": 1 = *Chlainomonas kolii* (collared cell); 2 = *Chlainomonas kolii* (cell lacking collar); 3 = *Chloromonas rubroleosa*; 4 = Chrysophycean cyst (with spout); 5 = *Chloromonas* sp. 3; 6 = other cell types (mainly unidentified cysts).

concentrations of cells there was considerable spatial variation within the bloom, shown by error bar size in Fig 4.3.14. The peak cell concentrations occurred at the end of sustained periods of melting (Fig. 4.3.5).

Red snow on the tarn surface in 1998 was made up almost entirely of three cell types (*Chlainomonas kolii* with and without the collared outer envelope, and *Chloromonas rubroleosa*). The former *Chlainomonas* cell type (Fig. 4.3.15) was almost always significantly higher than other types in the surface tarn snow when the

population was at low levels (paired t-Tests, $P<0.05$; days 14-27, 33-44). Increases of this cell type were accompanied by increases of the second *Chlainomonas* cell type, which dominated significantly at the end of the bloom (paired t-Test, $P<0.05$; Fig. 4.3.15, days 47-57).

Abundances in the surface 10 cm of tarn snow were greater than at other depths sampled in tarn snow or in shore snow at any depth (Fig. 4.3.5). Coloured bands in the snowpack below 10 cm depth were never observed. Abundance in tarn snow at 30-40 cm was much greater on day 14 than on any other day, and there was little variation among the six replicates. The total cell increase in the shore snow at 30-40 cm by the end of the study was due almost entirely to one small cell type (*Chloromonas* sp. 3). The only alga recorded at >10 cells ml^{-1} in any snow at 60-70 cm depth was the spouted chrysophycean cyst.

Algal cell concentrations during the 1999 study period were again significantly greater in tarn snow than shore snow (Fig. 4.3.16; Anova, $P=0.019$). Cell concentrations were also significantly different between days (Anova, $P<0.0001$). However, Tukey tests between total cell concentrations on individual days and Anovas on the separated data from each snow type showed that this variation was entirely due to differences in shore snow cell concentrations. Thus total abundance in tarn snow did not significantly differ between different days. Coloured snow was not observed on the tarn surface until day 14.

An additional cell type, *Chromulina* cf. *elegans*, was found in tarn snow in 1999. This alga was not recorded in direct counts from tarn snow the previous season, although it had previously been cultured from Mt Philistine snowfields. It may have been overlooked in 1998 if it only occurred in low numbers, as a result of its small size. *Chromulina* sometimes reached very high cell concentrations in tarn snow during the 1999 study period, especially below the surface (Fig. 4.3.17). It is separated from the "total" count because it has a much smaller biomass and highly variable distribution compared to the other snow algae.

Abundance of *Chromulina* was significantly greater in tarn snow than shore snow (Anova, $P<0.0001$), and abundances at 10-20 cm depth were significantly greater on day 13 than on day 19 (Tukey test, $P<0.05$). No significant effect of depth in snow was present in *Chromulina* temporal scale data.

Chlainomonas kolii (collared cell) remained significantly greater than other cell types (excluding *Chromulina*) in the surface tarn snow throughout the 1999 study

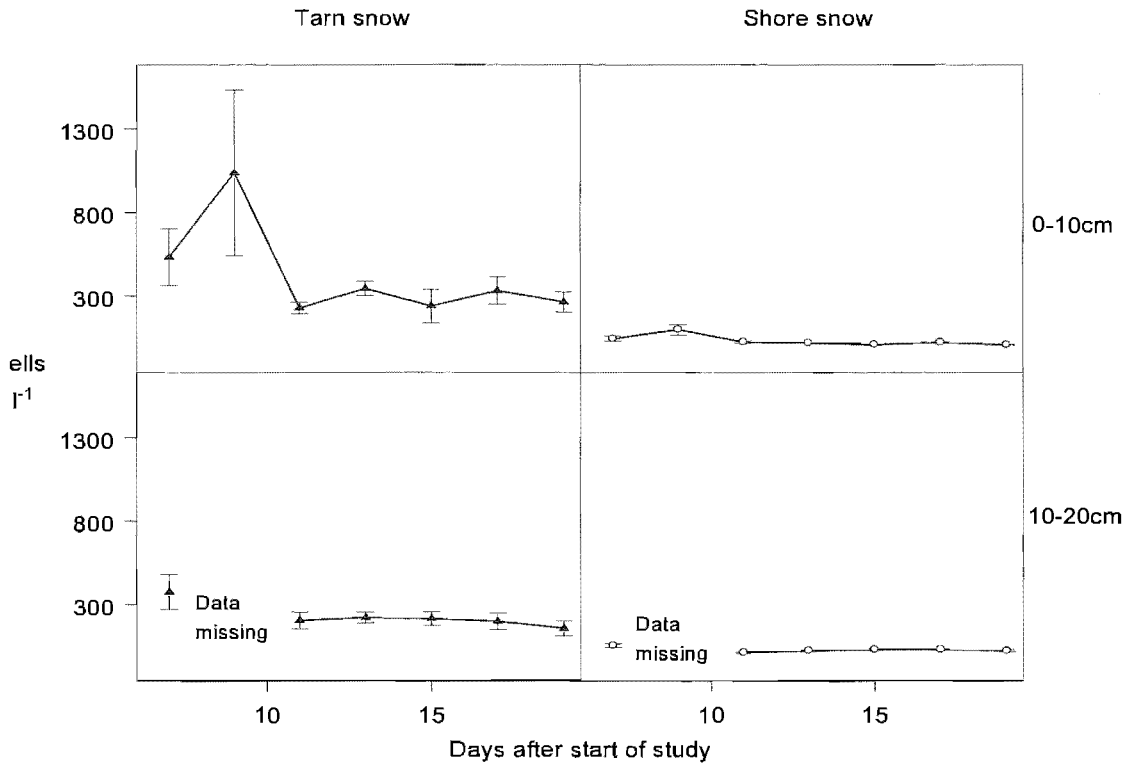


Fig. 4.3.16. Mean total cell concentrations of snow algal cells (excluding *Chromulina*; see Fig. 4.3.17) at the two sample depths from 1999 snow cores. Means are of 4 cores from each sample area. Error bars represent ±1 SE. Cell concentrations are direct counts of cells in melted snow samples and are not corrected for snow ablation over time.

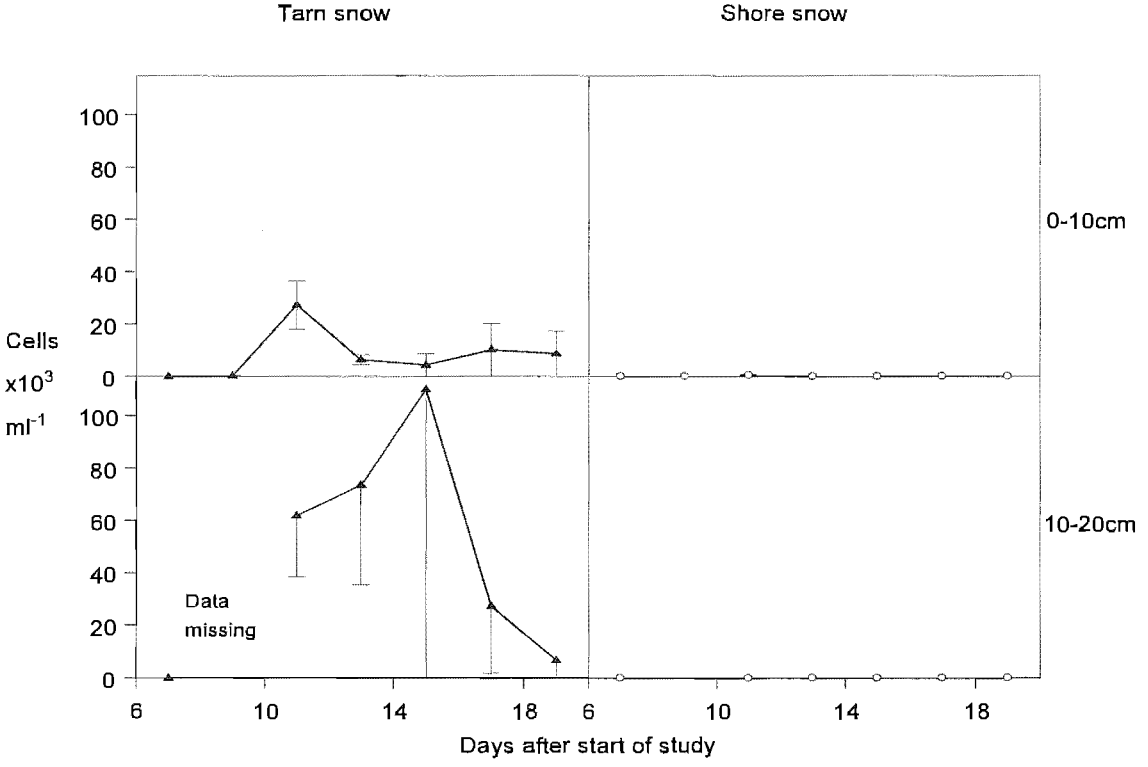


Fig. 4.3.17. Mean *Chromulina* cell concentrations at the two sampled depths from 1999 snow cores. Error bars represent ±1 SE (upper errors excluded at 10-20 cm in tarn snow for clarity). Means and samples as in Fig. 4.3.16.

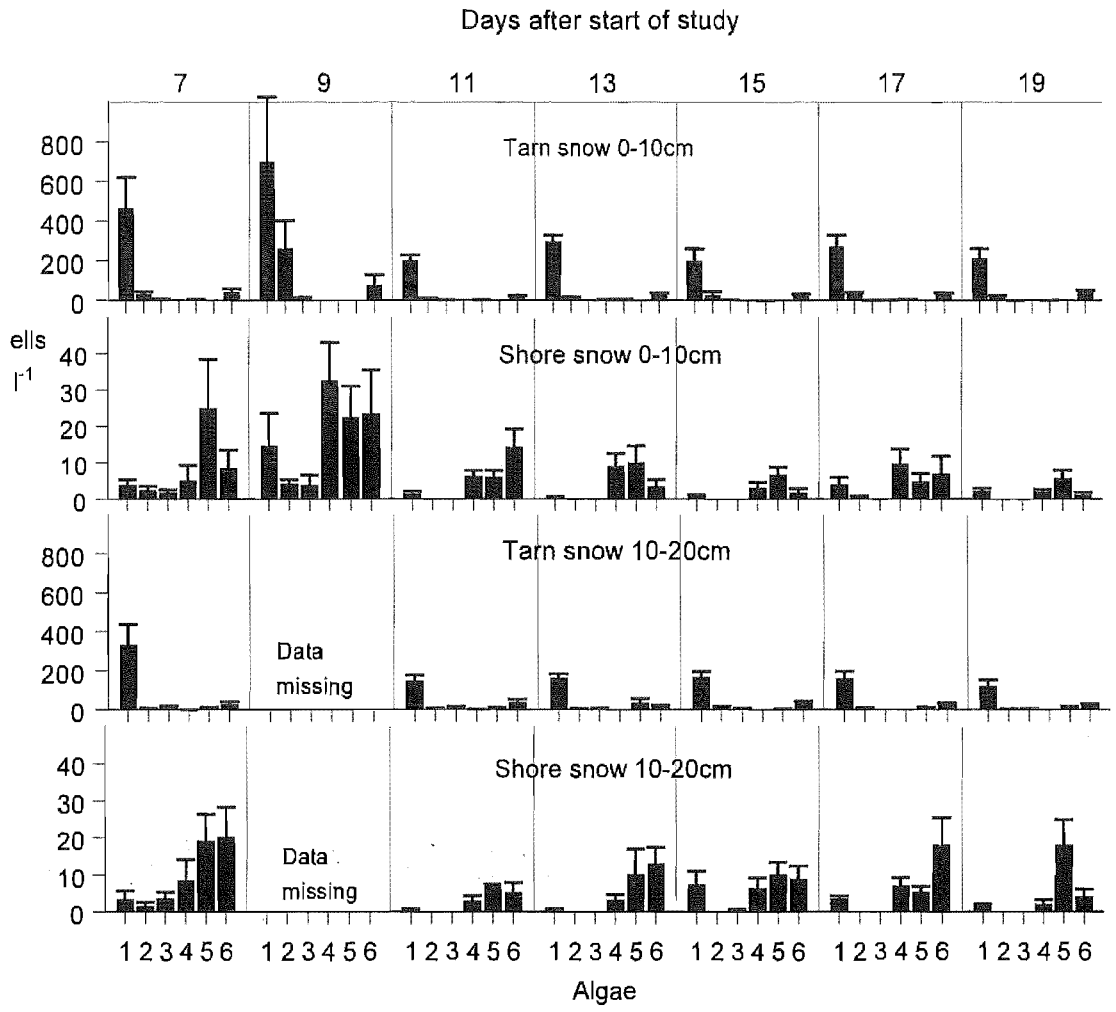


Fig. 4.3.18. Cell types in tarn and shore snow at the two depth ranges sampled, 1999 sampling period. Note different vertical scales in top two and bottom two panels. Errors represent ±1 SE. Data are means of 4 replicate counts. Concentrations refer to melted snow samples. Key to "Algae": 1 = *Chlainomonas kolii* (collared cell); 2 = *Chlainomonas kolii* (cell lacking collar); 3 = *Chloromonas rubroleosa*; 4 = Chrysophycean cyst (with spout); 5 = *Chloromonas* sp. 3; 6 = other cell types (mainly unidentified cysts).

period (Fig. 4.3.18; Tukey test, $P<0.05$). This cell type also dominated at 10-20 cm in tarn snow, but never reached high numbers in shore snow at any depth sampled.

About 90% of snow algae cells (excluding *Chromulina*) on day 13 of the 1999 study period occurred in the top 30 cm of tarn snow (Fig. 4.3.19). The maximum of 496±187 cells ml^{-1} was typical of both seasons in the tarn surface snow when an increase or decline was not occurring. The effect of depth on cell number was significant (Anova, $P<0.0028$). However, the Tukey test showed no significant difference between means from 0-10, 10-20, and 20-30 cm depth. Data from 0-10 and 30-40 cm in 1998 tarn snow (Fig. 4.3.14) fit the pattern observed in 1999.

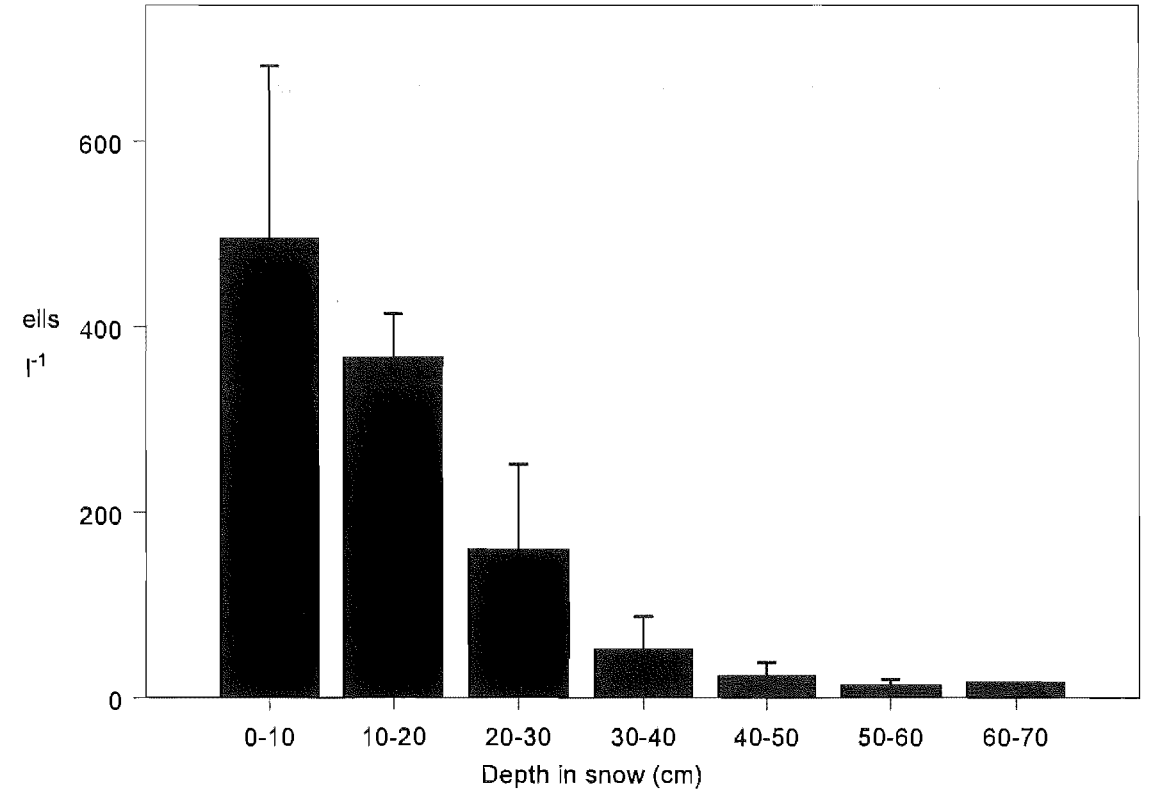


Fig. 4.3.19. Depth distribution of all snow algae other than *Chromulina* in tarn snow on day 13 of 1999 study period. Data are means of 3 replicates±1 SE.

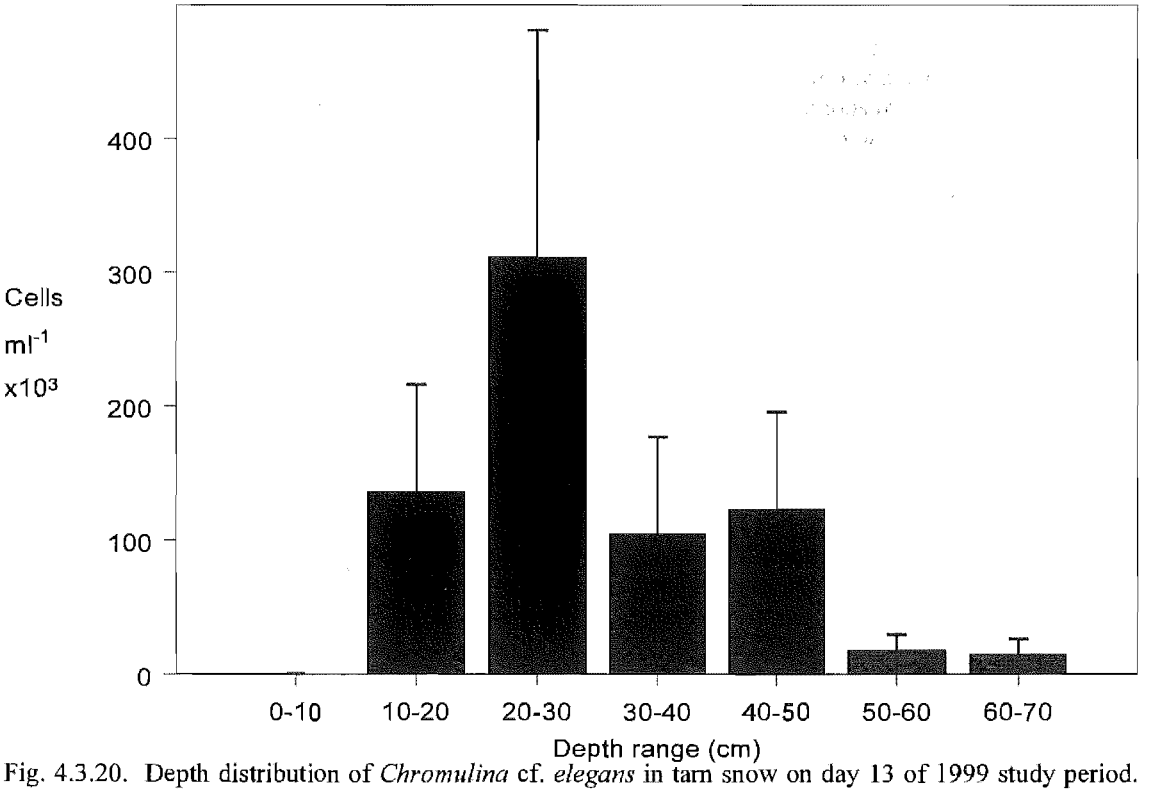


Fig. 4.3.20. Depth distribution of *Chromulina* cf. *elegans* in tarn snow on day 13 of 1999 study period. Data are means of 3 replicates±1 SE.

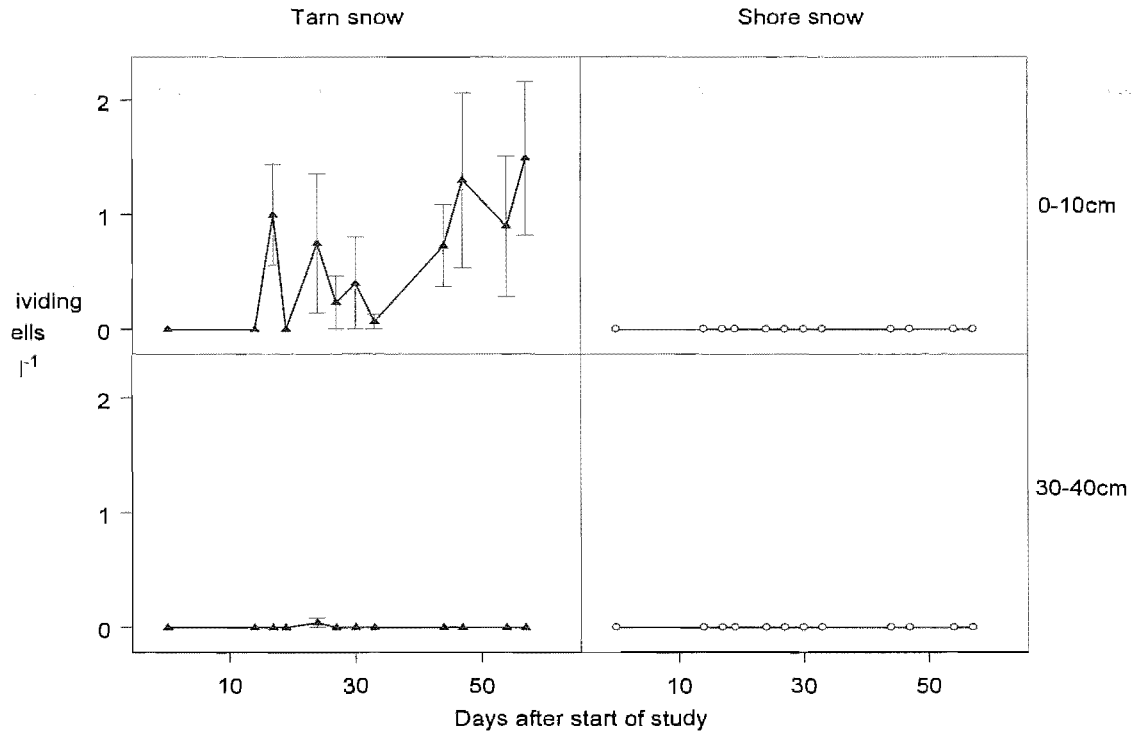


Fig. 4.3.21. Abundance of snow algal cells present as 2-, 4-, and 8-cell sporangia at 0-10 and 30-40 cm depth during 1998 study period. Data are means of up to 6 replicate counts ±1 SE. Most sporangia were of *Chloromonas rubroleosa*. Division of *Chromulina* cf. *elegans* was not visible in the counting chamber.

A different pattern was observed for *Chromulina* cf. *elegans*. The overall effect of depth on cell concentration was not significant (Anova, P=0.105)

Dividing cells found were 2-, 4-, or 8-celled autosporangia, mainly *Chloromonas rubroleosa*, and were low in numbers throughout both seasons (Fig. 4.3.21, 4.3.22). Two examples were seen of *Chlainomonas kolii* collared cells which appeared to be dividing. Abundance of dividing cells appeared to be higher in snow which contained a higher total cell concentration. Dividing cells were more common in 0-10 cm tarn snow than in other snow types. However, too few dividing cells were counted for their abundances between days to be validly compared.

Abundances of total cells in samples collected at 4 a.m. on days 7, 14 and 16 of the 1999 study period were significantly lower than those collected in daylight on the preceding days (Anova, P=0.001; Fig. 4.3.23). Tukey tests showed that this was due to a significantly lower total abundance in day 14 night samples. No *Chromulina* cells or any sporangia were observed in samples collected at night.

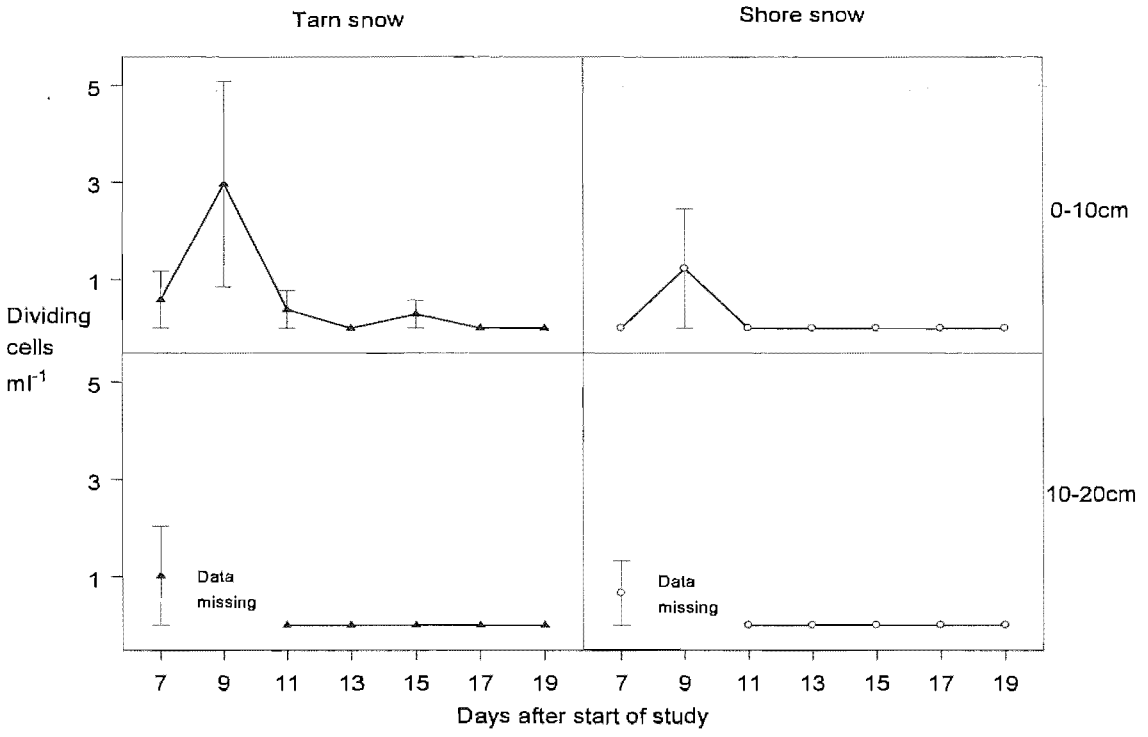


Fig. 4.3.22. Abundance of snow algal cells present as 2-, 4-, and 8-cell sporangia at 0-10 and 10-20 cm depth during 1999 study period. Data are means of 4 replicate counts ±1 SE. Division of *Chromulina* cf. *elegans* was not visible in counting chamber.

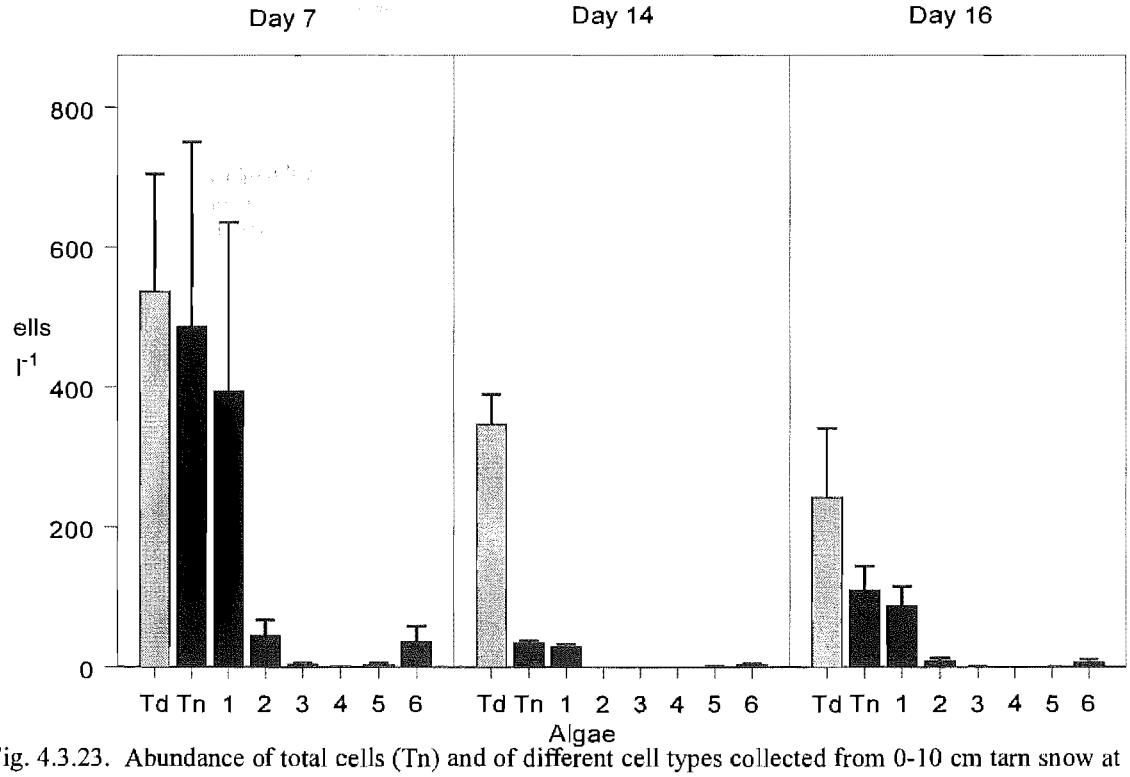


Fig. 4.3.23. Abundance of total cells (Tn) and of different cell types collected from 0-10 cm tarn snow at 4 a.m. on days 7, 14, and 16 of 1999 study period, compared with total abundance of cells in samples taken in daylight on preceding day (Td, light gray bar). Data are means of 4 replicate counts ±1 SE. Key to other algae: Tn = total cells in night sample; numbers refer to constituents of night samples: 1 = *Chlainomonas kolii* (collared cell); 2 = *Chlainomonas kolii* (cell lacking collar); 3 = *Chloromonas rubroleosa*; 4 = Chrysophycean cyst (with spout); 5 = *Chloromonas* sp 3; 6 = other cell types (mainly unidentified cysts). No cells of *Chromulina* or any sporangia were observed in these samples.

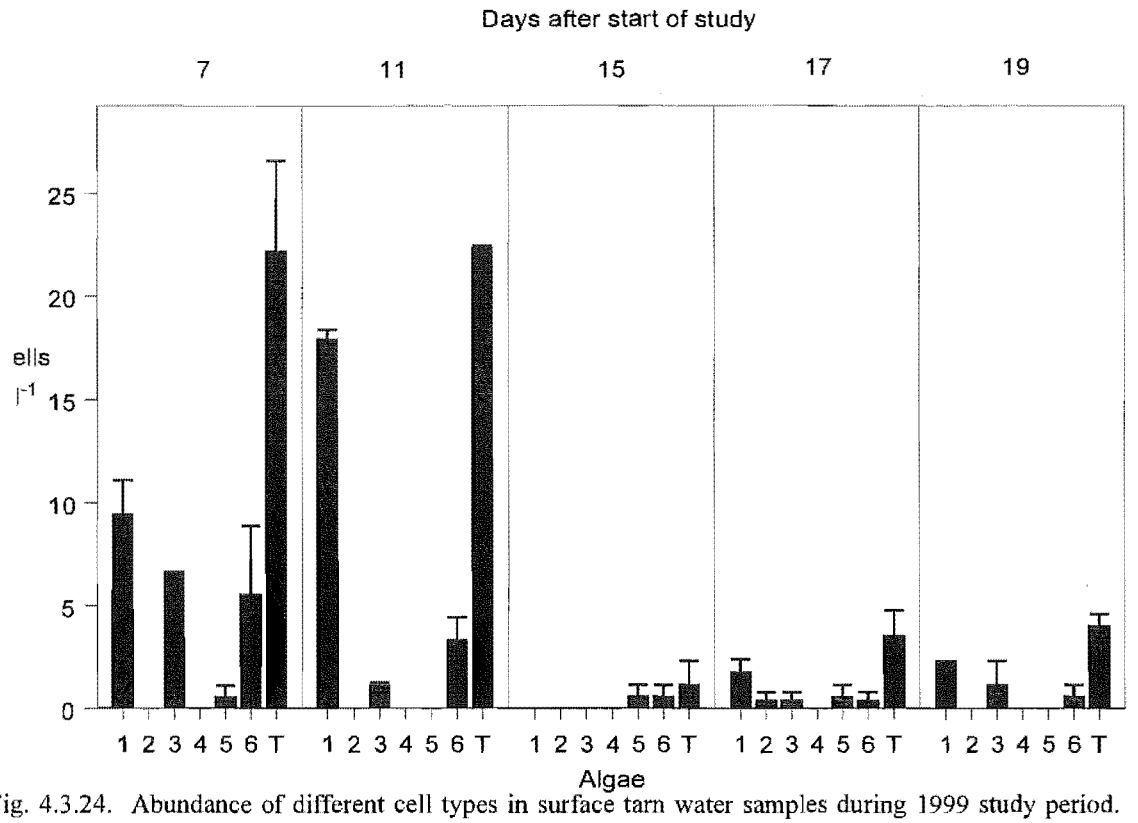


Fig. 4.3.24. Abundance of different cell types in surface tarn water samples during 1999 study period. Data are means of two replicate counts ±1 SE. Key to "Algae": 1 = *Chlainomonas kolii* (collared cell); 2 = *Chlainomonas kolii* (lacking collar); 3 = *Chloromonas rubroleosa*; 4 = Chrysophycean cyst (with spout); 5 = *Chloromonas* sp.3; 6 = other cell types (mainly unidentified cysts); T = total. No *Chromulina* cells were found in tarn water.

A maximum concentration of 22.2 ±4.4 snow algae cells ml^{-1} were found in water surrounding the tarn snow in 1999 (Fig. 4.3.24). Water with and without underlying snow was included in sampling. Collared *Chlainomonas* cells were dominant. *Chloromonas* sp.3, which dominated the shore snow community, was seldom recorded and the Chrysophycean cyst and *Chromulina* were never observed.

4.4. Discussion

4.4.1. Abundance of snow algae

Comparison with previous studies. The maximum mean concentration of 1.17±3.38 x 10^3 total cells ml^{-1} melted snow is lower than maxima reported previously for blooms of snow algae (Table 4.4.1). The maximum mean concentration observed in

Table 4.4.1. Typical cell concentrations in coloured snow blooms from different parts of the world reported by selected authors.

Authors	Location	Cells x 10^3 ml^{-1}	Dominant algae
Fogg (1967)	South Orkney Islands, maritime Antarctica	40	*Chlamydomonas*
Thomas (1972)	Sierra Nevada, California, USA	40	*Chlamydomonas*
Kol and Eurola (1973)	Van Mijenfjorden, Spitsbergen	10- 17	*"Scotiella"*[1]
Komarek (1973)	Belanske Tatra Mtns, Czech Republic	23-4638 8-858	*Koliella* *Chlamydomonas*
Hoham (1975)	Cascade Range, Washington, USA	400	*Chloromonas*
Mosser *et al.* (1977)	Beartooth Mtns, WY, USA	8- 14	*Chlamydomonas*
Hoham *et al.* (1979)	Utah, Colorado, Arizona, New Mexico, USA	500	*Chloromonas*
Akiyama (1979)	Antarctica	16- 53	*"Scotiella"*[1] + *Chlamydomonas* + *"Cryocystis"*[1]
Gamache (1992)	Lac Laflamme, Quebec, Canada	730(max.) 154(av.)	*Chloromonas*
Ling and Seppelt (1993)	Windmill Islands, Antarctica	200	*Chloromonas rubroleosa*

[1] Probably a resting cyst of a *Chloromonas* species.

1999 for *Chromulina* of 300±150 x 10^3 cells ml^{-1} is more typical. Since this alga is about an order of magnitude smaller in biovolume than *Chlainomonas*, the biomass of the two populations would be similar. Comparatively low population levels imply a suboptimal growth environment (see 4.4.4).

The *Chromulina* population was extremely patchy compared to *Chlainomonas* (see error bars in Fig. 4.3.16 and 4.3.17). Very high abundance in small localised zones may indicate germination of a relatively rare cyst, although which cyst this could be is uncertain. It is tempting to link *Chromulina* with the spouted Chrysophycean cyst which is found on Mt Philistine; however, there is no ecological basis for this linkage as the cysts were more common in shore snow, and virtually absent from tarn snow even at the end of the season (Fig. 4.3.15, 4.3.18).

Growth of the snow algae population – real or artifact? A melting snowfield concentrates material on its upper surface during melt by a process analogous to sediment collected from suspension on filter paper. Old summer snowfields are usually covered by a surface film of material which has been concentrated by this process. Fogg (1967) concluded that cell increases in the snow algae population he studied on South Orkney Islands, Antarctica, were due entirely to ablation of snow. Thomas (1972) found that Sierra Nevada snowfields were melting at 3-4 cm per day during his study, and mentioned its effect on cell concentrations. Kawecka *et al.* (1979) also commented on this possibility. Therefore, there are two possible reasons for the peaks in cell concentrations in Fig. 4.3.14 and 4.3.16. Were they due to growth *in situ*, or to ablation concentration?

Firstly, can the cell abundance increases theoretically be accounted for by cell division? During the second major increase in abundance during the 1998 study period (Fig. 4.3.14, top left panel, days 47-54), mean cell concentration increased from 250 to 1175 cells ml^{-1} over 7 days. This is equivalent to less than three doublings in 7 days or less than 1 division every 56 hours (0.4 divisions per day). Hoham (1971) found snow algae from Washington, USA, to undergo 0.25 divisions per day in culture. Ling and Seppelt (1993) found *Chloromonas rubroleosa* (also present on Mt Philistine) to undergo 0.25-0.33 divisions per day. Thus the apparent field division rates of the Mt Philistine snow algae, though not precise due to the size of the error, are similar to previous reports.

Cell abundance data for *Chromulina* in 1999 is more difficult to interpret. Large variability, reflecting a very patchy distribution, means that valid conclusions regarding growth rates cannot be made. This variability also justifies its exclusion from the total cell count, as it would obviously bias the other data.

Can snow ablation concentrate snow algae as it concentrates other material? Reports in the literature (Fogg 1967, Thomas 1972, Kawecka *et al.* 1979) suggest that it can. However, there is no direct evidence for this phenomenon on Mt Philistine, so any conclusion incorporating it must be made with caution.

If ablation of snow does concentrate cells, then it must make some contribution to abundance peaks in the surface snow, since snow depth loss was almost continuous throughout both study periods (Fig. 4.3.5, 4.3.6). Since it is very important to identify periods when the snow algae may have been growing, the possible extent of the contribution made to cell increases by snow ablation must be investigated. The most conservative method is to assume that all cells in a given depth of snow are

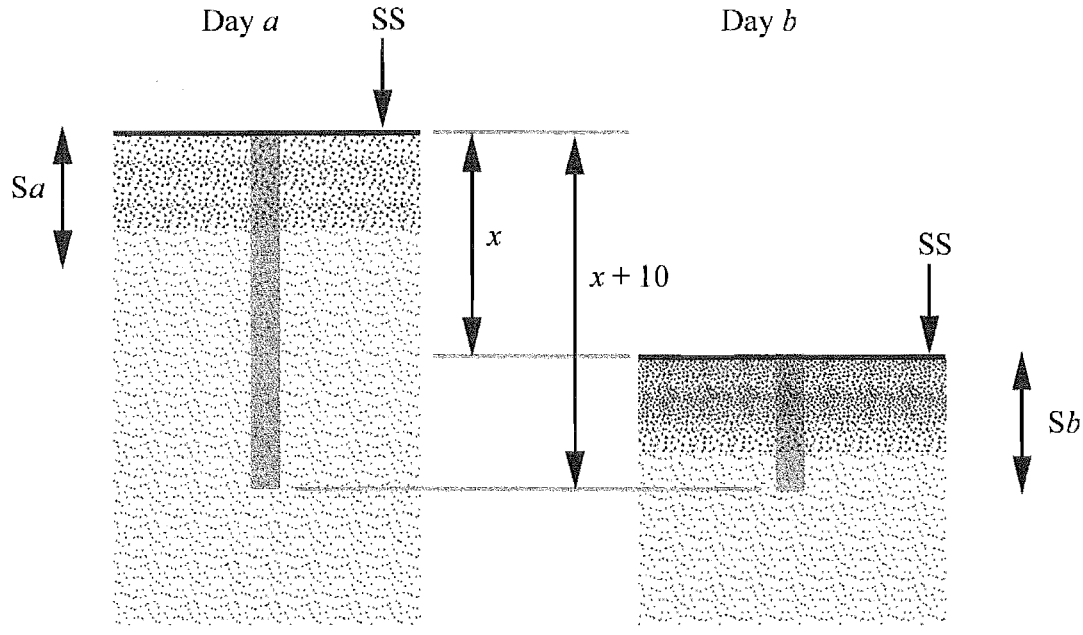


Fig. 4.4.1. Model of ablation concentration of cells used in correction equations (see Appendix 1). Dotted pattern represents snow algae. SS = snow surface. S*a*, *b* = 10 cm sampling depth on days *a* and *b* respectively. *x* = depth of snow lost by melt between days a and b. *x* + 10 = depth of snow on day *a* containing all the cells in S*b* on day *b*, assuming no cell loss and melting only from surface. Dark shaded rectangles represent longitudinal sections of rectangular prisms of snow with 1 cm^2 area in transverse section. They have corresponding total cell numbers of N*a* and N*b*, and cell concentrations per ml of C*a* and C*b*.

concentrated into the surface layer if that depth of snow melts, i.e. no loss of cells occurs during melt. Thus any cell increase not completely accounted for by such a calculation must have resulted from processes other than ablation concentration, such as growth. If the assumption that ablation concentrates cells is incorrect, a positive result (increase due to processes other than snow ablation) is not affected.

Suppose a loss of snow depth *x* occurs between days *a* and *b*. If the number of cells on day *a* in the top *x*+10 cm of snow is N_a and on day *b* in the top 10 cm is N_b, with associated concentrations per ml of snowmelt of C_a and C_b, then the amount by which N_b exceeds N_a shows the amount of increase which can be ascribed to processes other than snow ablation. This model is displayed diagrammatically in Fig. 4.4.1.

However, cell concentrations were only measured in the 1998 season from the depth ranges 0-10, 30-40, and 60-70 cm. Therefore more data are required if the effect of ablation concentration is to be determined. To fill gaps between these data, a formula was derived using the relationship of depth to cell concentration from day 13 of the 1999 study period (Fig. 4.3.19). The derivation and testing of this formula are presented in Appendix 1. The formula is:

$$y = (4.33a \times 10^{-4})x^2 - (4.67a \times 10^{-2})x + 1.26a$$

where y = cells ml^{-1} in snowmelt

x = depth (cm) in tarn snow

a = cell concentration in the surface 0-10 cm of tarn snow

for a given day during the snow algae bloom.

This equation describes one half of a parabola relating snow algae cell abundance (y) to depth in snow (x), and its slope is scaled by cell abundance in the surface snow (a). Although tests showed the formula to be less accurate at greater depth, most *Chlainomonas* cells in the snow column occur in the top 30 cm (Fig. 4.3.19), and erroneous calculations at greater depths make little difference to the result.

The equation was used to obtain a complete set of data for cell concentrations at 10 cm intervals throughout the whole snow column where necessary in both seasons, and used in terms of the model in Fig. 4.4.1. The results obtained are shown in Table 4.4.2.

Table 4.4.2. Correction for cell concentration by ablation of snow, using equation and method described in Appendix 1, for apparent growth peaks in both study periods.

Days (*a*-*b*)	C_a[3]	C_b[3]	Cell concentration not accounted for by ablation $(=C_b-C_a)$[3]
27-30[1]	166	753	587
44-54[1]	241	1175	934
7-9[2]	1016	1039	23

[1] 1998 study period; see Fig. 4.3.14.

[2] 1999 study period; see Fig. 4.3.16.

[3] C_a and C_b are cell concentrations on days a and b; units are cells ml^{-1} snowmelt.

The abundance of snow algae in both seasons remained at a relatively constant level for considerable periods of time (days 14-27 and 33-44, Fig. 4.3.14, and days 11-19, Fig. 4.3.16). During these periods ablation of snow was continuous (Fig. 4.3.5, 4.3.6). If it is assumed that snow ablation concentrates cells, it must follow that some cells are lost from the surface snow in order to maintain an approximately constant cell abundance during melt. Further evidence for loss of cells from surface snow was found for pollen and wind-dispersed algae blown onto snow (see Chapter 5: Dispersal, section 5.4.6).

A possible rate of cell loss can be calculated using the model in Fig. 4.4.1; the difference between C_a and C_b will thus be negative, and estimate cell concentration lost from the surface snow (Table 4.4.3). However, if the assumption that snow ablation concentrates cells is incorrect, the result of this calculation is invalidated..

Table 4.4.3. Maximum possible rate of cell loss from surface 10 cm of tarn snow over both study periods during apparent stationary phases. Method is described in Appendix 1.

Days (*a*-*b*)	N_a[3]	N_b[3]	Cells lost from surface snow (=N_a-N_b)	Rate of cell loss[4]
14-27[1]	1855	507	1348	20
33-44[1]	1545	566	979	16
11-19[2]	2975	1490	1485	33

[1] 1998 study period; see Fig. 4.3.14.

[2] 1999 study period; see Fig. 4.3.16.

[3] Total number of cells in column of snow 1 cm^2 in cross-sectional area, lost between days *a* and *b*.

[4] Units are ml^{-1} snowmelt day^{-1}.

In summary, the total cell count data (Figs. 4.3.14 and 4.3.16) can be interpreted in the following way in the light of information on snow ablation rates:

- neither of the abundance peaks recorded in the 1998 season are due solely to ablation of snow;
- rate of snow ablation associated with the abundance peak in 1999 data is such that it could potentially explain the entire apparent cell increase;

- it is possible that during relatively fine, stable weather cells are lost from surface snow at up to 16-33 cells ml^{-1} snowmelt day^{-1}.

Low numbers of dividing cells. Abundance of sporangia in all samples was very low in both seasons (Fig. 4.3.21, 4.3.22). However, it appears that cell division occurred between days 47 and 54 of the 1998 study period (Fig. 4.3.14, top left panel). The weather over this period included an unbroken 6-day storm from the north-west (Table 4.3.1), during which no samples were taken. It is therefore hypothesised that division occurs during major storms.

Sampling during the 1999 study period was undertaken in all types of weather during the day and night. However, although more than 200 mm of rain fell during the 1999 storm (Fig. 4.3.1), the period of rain was less than three days. This may have been insufficient time for the population to increase significantly, and the decrease in temperature indicated by snowfall at the end of the storm may have halted any growth that was occurring (see section 4.4.4).

The dominant collared cells of *Chlainomonas kolii* certainly divide (see Chapter 6: Taxonomy), as they have rarely been found forming autosporangia. One possible explanation for their virtual absence in surface tarn snow is that the algal population grows in tarn water, and cells collected in samples merely represent a proportion of the population deposited on snow following flooding. Low cell numbers in tarn water throughout the 1999 study (Fig. 4.3.24) show that this was probably not the case. Also, tarn water was never observed at a level high enough to account for all red snow observed.

4.4.2 Nutrients in Mt Philistine snow

Comparison with previous studies. The most abundant inorganic N species in Mt Philistine summer snow is NH_4-N (compare Figs. 4.3.7, 4.3.8, 4.3.9). The low but consistently detectable NO_3-N in the 1998 samples (Fig. 4.3.9) is probably due to dry deposition following snowfall, perhaps a unique dust deposition event in the 1998 season, since NO_3-N was seldom detectable in 1999. Dust inputs into snow are known to vary between years and seasons (Mayewski *et al.* 1987, Wagenbach *et al.* 1988, Gunz and Hoffman 1990). Wilson (1959a, b) related absence of NO_3-N in New Zealand winter snow to absence of terrestrial dust. The low to undetectable levels of NO_3-N in both seasons, and the dominance of NH_4-N in the inorganic fraction, confirm the results

of Wilson (1959a, b). Wilson (1959a, b) suggested that the combined N in New Zealand winter snow originated from the surface microlayer of the ocean. This has been suggested for NH_4-N in snow from elsewhere (Gunz and Hoffman 1990, Mayewski *et al.* 1987).

Concentrations of nutrients measured on Mt Philistine are generally lower than Northern Hemisphere values (Table 4.4.4). Very low nutrient levels in alpine snow containing algae have been reported in California (Thomas 1972). However, this was based on the analysis of a single sample. Ohtani *et al.* (1998), working in Antarctica, appear to have carried out the only Southern Hemisphere nutritional study on snow algae before the present. Their data are similar to the lowest Northern Hemisphere values. Presumably snow in Antarctica and New Zealand is less anthropogenically affected than Northern Hemisphere snow, accounting for lower concentrations of nutrients. It is likely that a large proportion of the NO_3-N present in North American snow originates as HNO_3 vapour from industry, which can be dry deposited to snowpacks and dissolve in precipitation (Cadle 1991, Lovett 1992, Murdoch and Stoddard 1992, Laird and Sommerfeld 1995).

Snow samples collected in Antarctica and alpine New Zealand are also less affected by forest cover than many of those reported in North America (Hoham and Mullet 1977, Hoham *et al.* 1989, Gamache 1992). Forest cover is known to increase nutrient levels in underlying snowpacks (Jones 1987, 1991, Cadle 1991).

Rigorous collection procedures are important when studying systems with low nutrient concentrations. For example, there was no preservation, filtration or constant freezing of the samples of Mueller *et al.* (1998) for 2-3 weeks following collection. Growth of psychrophilic bacteria could therefore explain the high variation in their samples, and possibly the absence of NO_3-N (Table 4.4.4). Often methods of collection or analysis are not described or referenced in papers (e.g. Komárek *et al.* 1973) meaning that reliability of results is unknown.

Concentrations of all three nutrients measured varied temporally and spatially within one area of red snow on Mt Philistine. High variability is a consistent feature of work on snow chemistry. For example, Tranter *et al.* (1987) found that surface snow of Ciste Mhearad, Scotland, was highly spatially variable in chemical composition within a small catchment (coefficient of variance 5-140%), sometimes over distances as small as 1 metre.

Nutrient utilisation. Active growth of the snow algae population was only convincingly observed during the 1998 season. Evidence for growth is fourfold. Firstly, abundance of cells in tarn snow peaked between days 47 and 54 (Fig. 4.3.14). Secondly, contribution of snow ablation towards concentration of cells is far insufficient to account for the observed increase (Table 4.4.2). Thirdly, a decrease in NH_4-N occurred in tarn snow during this cell increase. Such a nutrient decrease was absent from shore snow (Fig. 4.3.7), in which cell numbers were not increasing. Finally, a shift in dominant cell type occurred during this period (Fig. 4.3.15), consistent with a change in growth phase following utilisation of the nutrient resource.

If this interpretation is correct, then the abundance peak on day 9 of the 1999 data (Fig. 4.3.16), which is probably largely due to ablation (Table 4.4.2), should have no associated decrease in NH_4-N. Examination of Fig. 4.3.8 shows this to be the case. Lack of shift in cell dominance (Fig. 4.3.18), unlike in 1998 data, is additional evidence that this interpretation is correct.

Tarn snow is exposed to different physical processes than shore snow, such as water ponding for short periods following major storms (Fig. 4.3.4). There is no bulk movement of ions unique to tarn snow during these periods, because there is no significant difference between conductivity of tarn and shore snow (Fig. 4.3.12). Of course this conclusion relies on any physical processes which might occur affecting a substantial proportion of the ions in solution, since those measured were present in such low abundance that decreases did not affect conductivity. It does not rule out processes which may be specific to the nutrients measured in tarn snow; however, any such processes would be extremely difficult to detect by any method. Stable Cl^- concentrations, which have been used in the past to distinguish biological utilisation from physical movement (e.g. Gamache 1992), were not obtainable from the Mt Philistine samples because their concentrations were too low. In any case, Muller *et al.* (1998) found that Cl^- concentrations were higher in coloured snow than white snow in a large-scale survey in Svalbard. Their lack of preservation procedures should not have affected this result, since Cl^- is supposed to be biologically conserved (Jones 1991).

Unlike *Chlainomonas kolii* and *Chloromonas rubroleosa*, *Chromulina* cf. *elegans* was not recorded at all in tarn or shore snow populations in 1998. It is likely that the organism was present at lower abundance during 1998, but very unlikely that it

Table 4.4.4. Levels of NH_4-N, NO_3-N and DRP reported from snow associated with algal blooms in different parts of the world, compared with two seasons results from Mt Philistine.

Location	Nutrient concentration ($\mu g\ l^{-1}$)		
	NH_4-N	NO_3-N	DRP
Northern Hemisphere			
USA[1]	5.0	below detection	below detection
USA[2]	50	31200	130
Canada[3]	-	150	10
Canada[4]	-	-	329 - 670
Canada[5]	5830	868	0
Finland[6]	39000 -364000	21000 - 79000	7000 - 44000
Czech Republic[7]	0 - 4760	1300 - 3000	220 - 400
Svalbard[8]	180 - 5400	-	?
Southern Hemisphere			
Antarctica[9]	0 - 600	-[5]	0 - 600
New Zealand[10]	0 - 40	0 - 2.6	0 - 9.0
New Zealand[11]	5.8- 116	0 - 5.3	1.9- 5.6

- indicates no data reported.

? indicates data uncertain.

Authors: [1] Thomas (1972), [2] Hoham and Mullet (1977), [3] Gerrath and Nicholls (1974), [4] Hoham *et al.* (1989), [5] Gamache (1992), [6] Kol and Eurola (1973), [7] Komárek *et al.* (1973), [8] Muller *et al.* (1998b), [9] Ohtani *et al.* (1998), [10] Novis, 1998 data, [11] Novis, 1999 data.

[5] NO_3-N was present in one sample only.

would have been overlooked if it had reached concentrations comparable to those in the subsequent season.

During the 1999 study period, a significantly higher concentration of NH_4-N may have supported the growth of *Chromulina*. The organism is known to grow well at high nutrient levels, for example 250 mg NO_3-N l^{-1} in full strength medium. By comparison, *Chlainomonas kolii* was never successfully cultured and *Chloromonas rubroleosa* grew only in 5-20% strength medium (evidence is presented in Chapter 6

suggesting that *Chloromonas rubroleosa* and *Chlainomonas kolii* may be different cell types in a single life cycle).

Chromulina had no detectable effect on NH_4-N concentrations in tarn snow during the 1999 study period. Samples for nutrient concentrations were collected only from 0-10 cm depths of snow, and *Chromulina* populations seem to prefer greater depths (Fig. 4.3.17, 4.3.20). Also, no conclusions can be made regarding growth of the organism during the 1999 study period, due to its high spatial variability (see section 4.4.1).

NH_4-N is more efficient for cells to use than NO_3-N because an energy-consuming reduction to NH_4^+ is avoided. Some algae, such as *Chlorella vulgaris*, are known to stop NO_3^- assimilation in culture as soon as NH_4^+ is added (Pistorius and Funkhouser 1978). Also, the specific affinity of microbes for NH_4-N shows much less response to decreasing temperature than the specific affinity for NO_3-N, implying that at least some uptake of NH_4-N occurs passively (Nedwell 1999). Therefore, it is not surprising that NO_3-N does not appear to play a role in nutrition of snow algae on the Mt Philistine tarn. Although Hoham *et al.* (1989) found that NO_3-N concentrations were low in snow containing large numbers of resting cysts relative to other snow, Hoham (1971) found greater abundances of *Chloromonas pichinchae* and *Raphidonema nivale* at the end of growth phase in culture when the inorganic N source was NH_4-N rather than NO_3-N.

According to Jones and Sochanska (1985), DRP in a snowpack indicates heterotrophic microbial activity. If this is true then more DRP would be expected in snow under trees than in open areas, as reported by Hoham (1976). Therefore, the absence of inorganic P in snow analysed by Gamache (1992), also working in a forested system, seems surprising. DRP on Mt Philistine is generally lower than reported in previous studies (Table 4.4.4). No utilisation by cells was detectable, and differences in concentration between days are not easy to correlate with any other factors measured. The significantly higher DRP recorded on day 47 of the 1998 study period cannot be linked to bacteria associated with the algae population (Thomas and Duval 1995), because it occurred in both shore and tarn snow (Fig. 4.3.10).

Theoretical nutrient requirements. The requirements of 0.04 pg N μm^{-3} and 0.005 pg P μm^{-3} have been calculated from dry weights of a variety of cultured algae (Reynolds 1984). The volume of a prolate spheroid (Hillebrand *et al.* 1999) can be used to estimate the biovolume of a single *Chlainomonas kolii* cell of mean diameter and length

(see Chapter 6), and thus the N and P required to support the biovolume of algae in the snow samples. This calculation gives requirements of 200 μg N l^{-1} and 29 μg P l^{-1}, clearly higher than the measured values in the snow.

If culture represents optimal growth conditions, this result indicates that nutrients may be limiting in the Mt Philistine snow. However, field populations can be supported by nutrient levels considerably lower than cultured populations (Reynolds 1984), from which the theoretical nutrient requirements were derived. Additional complicating factors are the decreased affinity for substrates at lower temperatures (Nedwell 1999), which means that detectable concentrations of nutrients at low temperatures may still be limiting, and the dispropotionate concentration of nutrients in meltwater spaces in the snow (Table 4.3.4).

Some snow algae are capable of utilising simple organic nitrogenous compounds (Hoham 1971). The concentrations of such compounds and the ability of algae to utilise them in Mt Philistine snow are completely unknown. Wilson (1959a, b) recorded organic N of up to 200 μg l^{-1} in New Zealand winter snow. Some of this material may be bioavailable, and account for part of the apparent discrepancy between theoretical and measured N concentrations. Perhaps such compounds are metabolised only when inorganic sources of N are exhausted, similar to preferential use of NH_4-N over NO_3-N (Pistorius and Funkhouser 1978). Analysis of further samples is required to test this suggestion.

A number of problems also exist for interpreting DRP results. Firstly, a low measured DRP does not necessarily mean a limiting concentration, because regeneration of phosphate from organic forms of P can be rapid in freshwater systems (Lean 1973, Elser and Kimmel 1985). Algae are also capable of taking up phosphate well below the levels of detection (Graham and Wilcox 2000). Thus it is quite possible for regeneration to mask utilisation.

It was long assumed that DRP is equivalent to orthophosphate, but is has since been shown that the acid molybdate method overestimates orthophosphate (Bostrom *et al.* 1988). DRP fractions (also known as SRP or MRP) contain high molecular weight compounds and "colloids", i.e. compounds differing from the orthophosphate ion (White *et al.* 1981, Broberg and Persson 1988). It is thus clearly erroneous to equate DRP with the immediately biologically available orthophosphate ion. Further discussion of the nature of DRP and its bioavailability can be found in White *et al.* (1981), Bostrom *et al.* (1988), Broberg and Persson (1988), and Haygarth *et al.* (1997).

A relatively large amount (greater than 50%) of the reactive material analysed in the Mt Philistine samples probably represents some form of bioavailable phosphorous. The results must be interpreted in this context. Snow algae did not detectably utilise the measured P fraction, possibly because the analysis was not a close enough approximation of the bioavailable fraction at such low concentrations. The possibility of bioavailable organic P being present but undetectable using the acid molybdate technique (Bostrom *et al.* 1988) may account for part of the discrepancy between theoretical and measured concentrations.

Results from 1998 (Figs. 4.3.7, 4.3.9, 4.3.10) suggest that the baseline level of nutrients required for growth is not high, at least in the case of those nutrients measured. Nutrients may be supplied adequately for *Chlainomonas kolii* by frequent inputs of precipitation (Barry and Price 1987), atmospheric dust, and possibly pollen (which can reach quite high levels in Mt Philistine snow, as discussed in Chapter 5). Hoham and Mullet (1977) considered pollen and dust to be possible nutrient sources for snow algae. Large amounts of nitrogen (up to 0.796 mg inorganic N l^{-1} in rain, and up to 0.079 mg l^{-1} in fresh snow that was not influenced by birdlife) can be present in Antarctic precipitation (Greenfield 1992).

Change in life cycle stage of *Chlainomonas kolii*. Abundance of *Chlainomonas kolii* increased in 1998 between days 54 and 57 (Fig. 4.3.14), with a subsequent decrease in cells surrounded by an outer reticulate envelope and an increase in cells in which this was lacking (Fig. 4.3.15). Loss of the envelope followed, rather than preceded, the growth phase, as suggested by the following lines of evidence.

Firstly, total abundance of enveloped and non-enveloped cells remained similar during envelope loss. Secondly, no cell division was ever observed in non-enveloped cells, but was observed in cells surrounded by an outer envelope. Thirdly, loss of the outer envelope has frequently been observed in field samples without any evidence of cell division.

Hoham (1971) suggested that NO_3-N concentrations were important in snow algae growth in the field, because NO_3^- was utilised by the population which then developed into sexually (or asexually) produced resting stages when it became depleted. Hoham's studies have been based on *Chloromonas* species, the life cycles of many of which are now well understood (Hoham 1975, Hoham and Mullet 1977, Hoham *et al.* 1979, 1983). At present no sexual reproductive cycle is known for *Chlainomonas kolii* unless the cells identical to *Chloromonas rubroleosa* can be implicated in the life cycle

(see Chapter 6). These cells were usually less than 10% of total abundance in the field (Fig. 4.3.15, 4.3.18). Therefore the hypothesis of Hoham (1971), proposed for *Chloromonas* under North American conditions where NO_3-N is considerably more abundant, remains to be tested.

Clearly NO_3-N is not involved in the cell type shift in *Chlainomonas kolii*. However, low NH_4-N conditions (Fig. 4.3.7, day 54) could be linked to the loss of the outer envelope.

Seasonality of nutrient concentrations. The concentration of NH_4-N in the 1998 bulk snow (Fig. 4.3.7) was significantly lower than in 1999 (Fig. 4.3.8). It is possible that this is related to the time of year at which the NH_4-N was measured. A significantly higher concentration of nutrients in the snow would be expected earlier in spring, due to the phenomenon of preferential elution (Table 4.3.4; Johannessen and Henrikson 1978, Colbeck 1991).

However, the dynamic and heterogeneous nature of snow (Adams 1981, McKay and Gray 1981, Granberg 1985, Colbeck 1987, Tranter *et al.* 1987, Pomeroy *et al.* 1991; shown by variability in measured nutrients among and between replicates in each season) makes conclusions regarding seasonality difficult to justify. Any effect of season may be masked by this day-to-day variability, and two complete data sets would be required for a valid comparison between seasons. This heterogeneity is the greatest obstacle to progress in observational ecology on snow communities. Although the snow algae population developed earlier in 1999 (compare Fig. 4.3.16, where the maximum cell concentration occurred on 16 November, with Fig. 4.3.14, where comparable cell concentrations were not reached until 24 December), there is no evidence that nutrient levels influenced initiation of the bloom. Rather, it seems that the stage of melt and breakup of the surface snow was responsible (see below).

The situation differs in North America (e.g. Gamache 1992), where snow algae blooms follow release of the first polluted and acidic fraction of melt from the snowpack. NO_3-N concentrations are low enough in Mt Philistine snow, however, to indicate that no acidifying HNO_3 is present to affect timing of the snow algae bloom (Table 4.4.4).

Snow melt, liquid water content (LWC), and possible effects on nutrient levels. Snow algae on the Mt Philistine tarn have been observed over three consecutive seasons. In each season, development of the population seems to have been related to

the stage of melt of the snowpack. In summer 1997-98, melting did not reach an advanced stage (large blocks of snow in the tarn surrounded by open water) until mid-January. This stage was reached earlier in successive seasons: mid-December and late November in 1998 (Fig. 4.3.4) and 1999 respectively.

Earlier melting was due to the presence of less snow at the end of winter in each successive season. This can be seen by comparing Fig. 4.2.1d (27 November 1998) and f (15 November 1999). Snowfield retreat at several sites during 1998 (Fig. 4.3.3) suggests that a large amount of snow present initially buffers the effect of melting by reducing solar heating of dark ground surfaces which extend beneath the snow. When rocks emerge through the snowpack, melting around their edges rapidly fragments the snow and the snowfield disappears much faster. The same is true of slopes surrounding the tarn: melting on the tarn surface can reach an advanced stage more quickly under the same weather conditions when less snow is present at the start of spring melt.

In 1998, unusually for the Southern Alps, there was little rain during November (Table 4.3.1), whereas November 1999 was characterised by high rainfall, especially early in the month (Table 4.3.2). A greater amount of precipitation fell as snow in 1998 compared to 1999. Fig. 4.3.5 and 4.3.6 show the strong influence of rain on snowmelt. Note that a large snowfall occurred in early December 1998 which briefly restored snow depth almost to initial depth. Therefore, differing weather conditions during the two seasons probably contributed to the earlier bloom development in 1999.

Numerous papers acknowledge the importance of snow LWC for growth of snow algae (e.g. Fogg 1967, Hoham 1971, 1975, Hoham and Mullet 1977, 1978, Kawecka 1978, Hoham *et al.* 1979, Kawecka and Drake 1981, Hoham and Mohn 1985, Jones 1991, Muller *et al.* 1998). However, little data have been collected on this relationship (section 4.1.4). Large inputs of rain can greatly increase LWC of tarn snow, but not shore snow (Fig. 4.3.13). Rain on a Mt Philistine terrestrial snowpack is rapidly absorbed and drained away from surface layers, which remain comparatively dry. The Hydrosense probe was unable to detect any difference in LWC of shore snow under any weather conditions. In contrast, snow overlying tarn water causes water to pond near the snow surface, probably due to ice layers associated with water below the surface; hence the dramatic, though variable, increase in tarn snow LWC during heavy rain.

The first fractions of meltwater experimentally eluted from spring snow samples contained greater concentrations of NH_4-N than bulk snow (Table 4.3.4). This implies

that greater nutrient concentrations are present in interstitial water spaces occupied by algae than those indicated by analysis of bulk snow samples.

It has been reasoned (section 4.4.1) that minimal growth of the *Chlainomonas* population occurred throughout the 1999 sampling period. Without the influence of algal utilisation as in 1998, NH_4-N in tarn snow remained similar to that in shore snow (Fig. 4.3.8). However, it is likely that rainwater melting the tarn snow by ponding would increase concentrations of nutrients in interstitial water (Table 4.3.4) relative to that in shore snow, the LWC of which remains lower during rain (Fig. 4.3.13). It is possible for snow on the surface of a lake to become increasingly concentrated in nutrients as meltwater becomes trapped in slush layers above a layer of ice (Tranter 1991).

Under fine weather conditions such an enrichment effect may be insignificant, as LWC in surface snow is very low (less than 10% by weight, Fig. 4.3.13). However, during heavy rain when tarn snow LWC increases, the effect could be considerable. For example, NH_4-N concentration in tarn snow on day 9, 1999 (Fig.4.3.8), although appearing the same as the previous day in bulk snow terms (approx. 27$\mu g\ l^{-1}$), would be expected to be considerably higher in interstitial spaces given its LWC on that day (approx. 28%, Fig. 4.3.13). The maximum concentration factor of 3.9 in experimentally eluted meltwater from the tarn snow (Table 4.3.4) suggests a concentration of more than 100 $\mu g\ l^{-1}$. This is much closer to the theoretical requirement for growth (see above) than the concentrations obtained from analyses of bulk snow.

4.4.3. Light

About 90% of *Chlainomonas kolii* occur in the top 30 cm (Fig. 4.3.19, 4.3.15), whereas most *Chloromonas* sp. 3 were found at 30-40 cm (Fig. 4.3.15, compare shore snow 0-10 and 30-40 cm, days 44-57), and greater abundances of *Chromulina* cf. *elegans* were found below the surface 0-10 cm (Fig. 4.3.17, 4.3.20). Therefore, different snow algae are distributed at different depths in the snow. Whether preference for different light intensities or some other factor causes these different distributions is uncertain.

Light climate has been regarded as a factor regulating areal distribution of certain snow algae. For example, Hoham and Blinn (1979) found *Chlamydomonas nivalis* to dominate in open exposures and *Chloromonas nivalis* to dominate in snow shaded by trees. The effect of tree shading in New Zealand is absent, because the spring

and summer snowline does not persist below the treeline (see Chapter 2). Clearly, shaded slopes in New Zealand are more likely to contain snow algae because snow is retained longer on shaded, south-facing slopes. The general aspect of the Mt Philistine study site is towards the south (see Chapter 2).

Nonetheless, incident light levels on Mt Philistine are generally much higher than in snow covered by forest. Hoham (1975) measured incident light levels during collection of *Chloromonas pichinchae*, a snow alga which is never exposed to full sunlight (Hoham, pers. com.). The results can be converted to quantum units with reasonable accuracy by extrapolating Hoham's measurements of total energy at three wavelengths of light to fill the visible spectrum, then calculating energy per photon according to methods described by Gates (1980). The number of photons and their molar flux (quantum units) can then be calculated. This procedure gives a mid-day reading of 1965 μmol m^{-2} s^{-1} under clear sky conditions from Hoham's data. This is a similar value to mid-day incident readings taken on Mt Philistine in fine weather (Table 4.3.3). However, Hoham's measurements at 0820-0835 hrs under high overcast conditions convert to only 135 μmol $m^{-2}s^{-1}$. Presumably this shows the effect of shading by trees when the sun is not at its peak.

Incident photon flux on Mt Philistine under clear sky at 0800hrs is still up to 2000 μmol $m^{-2}s^{-1}$ during November-December (data not shown). The thickest cloud during fine weather gives readings of 600-800 μmol $m^{-2}s^{-1}$ at midday (Table 4.3.3). Photon flux during storm conditions on day 10 of the 1999 study period was approximately 170 μmol $m^{-2}s^{-1}$ at midday (Fig. 4.3.2, converted to quantum units by calibration factor between sensors of 1.66). This maximum is still slightly higher than the value recorded by Hoham (1975) under shade at 0820-0835 hrs.

Are light levels too low for growth of snow algae to occur during storms on Mt Philistine? The 1998 results suggest that they are not. The growth period shown in Fig. 4.3.5 occurred during 6 days of continuous cloud with rain (days 47-54, Fig 4.3.1). Presumably light levels during this period were similar to those during the storm of 1999 (Fig. 4.3.2). Therefore *Chlainomonas kolii* can grow on Mt Philistine during storm conditions, when photon flux is considerably lower than during fine weather.

Chlainomonas kolii has previously been found only in forested areas of North America (Hoham 1974a). The difference in incident light between such an environment and that on Mt Philistine appears striking, but only during fine weather. Clearly the two environments are much more similar if storm conditions on Mt Philistine are considered. Because growth of the New Zealand organism is proposed to occur under

these storm conditions (see section 4.4.1.c), it seems that the New Zealand and North American populations may be exploiting remarkably similar light environments.

Further support for this suggestion is available. Bidigare *et al.* (1993) hypothesised that production of red pigment by snow algae is a response to high irradiance under low nitrogen conditions (see section 4.1.4). If this hypothesis is correct, any red snow algae cells synthesising the red pigment must be exposed to light in excess of that which can be used for photosynthesis under the current nutrient conditions. *Chloromonas rubroleosa*, when grown in culture at light levels considerably lower than those experienced in the field and with inorganic N somewhat higher, slowly lost the red pigment over time, and last to be masked by pigment was the nuclear region. The same observation has been made with *Chlamydomonas nivalis* (Hoham pers. com. and 1980). Therefore the incident light levels during storms on Mt Philistine may actually be a respite from light levels during fine weather which are high enough to inhibit growth.

Photoinhibition is difficult to measure since it is related to time of exposure to the light source (which is often short experimentally). It can be hidden in whole-community incubations, and UV-absorbing chambers may remove short-wave radiation, which may also not be emitted by laboratory lamps (Hill 1996). The importance of UV-A and UV-B on photoinhibition of phytoplankton in Lake Erie was demonstrated by Marwood *et al.* (2000), who found that short exposure to 1222 μmol $m^{-2}s^{-1}$ PAR had no inhibitory effect without the environmental short-wave radiation.

In benthic freshwater algae, photoinhibition is often reported above 600 μmol $m^{-2}s^{-1}$, and typical light saturation for photosynthesis is below 400 μmol $m^{-2}s^{-1}$ (Hill 1996). Exposure to about 700 μmol $m^{-2}s^{-1}$ in culture is reported to cause photoinhibition in *Anabaena flos-aquae* (Young and Yull 1999), and 2000 μmol $m^{-2}s^{-1}$ does so in *Dunaliella salina* (Polle and Anastasios 1999). If these values are comparable to snow algae then clearly the total photon flux of over 5000 μmol $m^{-2}s^{-1}$ in surface snow during fine weather should be inhibitory (Table 4.3.3). Susceptibility to photoinhibition can also be increased at low temperatures, such as 5°C in the red alga *Lomentaria orcadensis* (Kuebler *et al.* 1991), although it has been suggested that the low temperatures of ice habitats can reduce its effect on adapted organisms (Markin and Nikitina 1983).

4.4.4. Amenable growth conditions

Red snow dominated by *Chlainomonas kolii* on Mt Philistine forms only on surface snow of the large tarn. Clearly one or more factors exist in this snow which create favourable conditions for growth. It is important to note, however, that this exceptional snow environment is not exploited on Mt Philistine to such an extent by *Chloromonas* or *Chlamydomonas* species (Wilson 1976, Thomas and Broady 1997) which are more common in long-lived terrestrial snowfields, such as those further south in Mt Cook National Park.

In March 1997 a red snow bloom consisting entirely of the spouted Chrysophycean cyst was observed in the upper basin on Mt Philistine, yet these cells have been seldom observed in tarn snow. Similarly, *Chloromonas* sp.3, the dominant alga at 30-40 cm depth in shore snow (Fig. 4.3.15), was rarely seen in tarn snow. Clearly the ecological preferences of these organisms are varied and complex, and extension of any conclusions regarding the growth environment of *Chlainomonas kolii* to include other snow algae would be completely unjustified.

Only Thomas (1971) specifically refers to snow algae growing in snow on the surface of a tarn, in the Sierra Nevada, USA. Red snow blooms have been reported from several other tarns in the Southern Alps of New Zealand, including at Lake Crucible, Mt Aspiring National Park (Lord pers. com., Gerbaux pers. com.), below Mt Oates, Arthur's Pass (Broady pers. com.), and on the Douglas Glacier, Arrowsmith Range (Wiles pers. com.). My work seems to be the first time that tarn snow algae have been studied in detail. Clearly the conditions on the Mt Philistine tarn are not unique, and this particular environment is amenable for growth of some species at certain times. Red snow has also been noted on pack ice and floes in the Arctic and Antarctic (Graham and Wilcox 2000). This may be a related phenomenon, if layering in sea ice allows water ponding, as occurs in the tarn snow.

Hoham (pers. com.) has suggested that the ecology of *Chlainomonas kolii* is "somewhat different from that of other snow microbes". My results confirm this view, at least for the Mt Philistine cryoflora. Further discussion on identity of the organism and whether it is the same as that reported from North America (Hoham 1974, 1980) is included in Chapter 6 (Taxonomy).

Conditions on Mt Philistine are generally not amenable to growth of snow algae. Even in the bloom-forming population, cell numbers are considerably lower than those reported elsewhere (Table 4.5.1). This may be partly due to lower nutrient levels (Table

4.5.9), but most important are the conditions which determine the ability of algae to utilise them, since detectable nutrient levels are nearly always present, but recognisable population growth is not. Decrease in substrate affinity at low temperature means that detectable nutrient concentrations may still be limiting growth (Nedwell 1999).

Apart from its effect on nutrient levels, LWC may be important as an indicator of non-freezing conditions. Apart from risk of cellular disruption at temperatures below 0°C, freezing represents a LWC of 0%. Freezing of surface layers of the snowpack always occurs at night during clear sky conditions in November-December on Mt Philistine.

During rain, however, no freezing occurs. In such conditions, the combined effect of higher nutrient availability (section 4.4.2f), lower light levels (section 4.4.3), and available liquid water (section 4.4.2f) may be important for growth of the *Chlainomonas* population.

Comparison with North American forested conditions is illuminating. When Hoham *et al.* (1983) collected *Chloromonas polyptera*, air temperatures had remained above freezing for several weeks. When Hoham and Mullet (1977) collected *Chloromonas nivalis*, air temperature varied between 3-26°C over 1 week. Such conditions do not exist on Mt Philistine during fine weather. Continuous rain is the only time when overnight freezing of the surface snow has not been observed during November and December. On Mt Philistine, continuous rain is nearly always accompanied by thick cloud and very strong winds, creating difficult study conditions.

Freezing of surface snow may have resulted in the significant difference in cell concentration between day and night samples on days 13/14 (Fig. 4.3.23). A brief snowfall from the south (Table 4.3.2) occurred on day 13 which caused the surface snow to be frozen extremely hard at 4 a.m. on day 14. In contrast there was no freezing on days 6/7, and a lesser freeze on days 15/16. Cells of *Chloromonas nivalis* were found by Hoham (1975) to migrate vertically by up to 15 cm on a diurnal basis. Vertical migration in *Chlamydomonas nivalis* appears to be light-related and enabled by changes in the ability of cells to attach to the surface of snow crystals (Grinde 1983). Perhaps temperature reduction could act as a trigger for a similar mechanism in *Chlainomonas kolii*, causing migration of cells down through the snowpack.

Protoplasts of *Chlainomonas rubra* are damaged by freezing (Hoham 1974b). It is possible that the net-like outer envelope of *C. kolii* (Chapter 6; see also Hoham 1974a, 1980) is involved in prevention of freezing of the protoplast. However, *C. kolii*

from North America is found in forested regions (Hoham 1974a), which are presumably less subject to diurnal freezing during the growth season.

A further question must be addressed. Given that LWC was high in the snow and available nutrients were present during the 1999 study period, why were they not utilised? Possible answers are forthcoming by examination of conditions prior to and during the growth phase in 1998 (days 47-54, Fig. 4.3.14).

The growth period consisted of 6 days of rain (Table 4.3.1), which caused the most rapid melt of the season (Fig. 4.3.5), at a higher rate than that reached in 1999 and sustained for considerably longer (compare Fig. 4.3.5 and 4.3.6). The largest areal melt of snow also occurred during this period (Fig. 4.3.4). North-west rain is known to cause the fastest snow melt in New Zealand alpine conditions (Prowse and Owens 1982). Heavy rain caused an increase in tarn snow LWC in 1999 (Fig. 4.3.13). This may result in higher levels of NH_4-N in tarn snow than in shore snow (Fig. 4.3.8), an effect not observed in 1998, perhaps because the algal population in 1998 was acting as a sink for NH_4-N.

In comparison, the 1999 population was exposed to 3 days continuous rain (days 8-10, Table 4.3.2), the final day of which fell as snow. Therefore, although the amount of rain was high (Fig. 4.3.1), its duration was comparatively short. The estimate of doubling time (once every 56 hours, see section 4.4.1b) would allow an average of only one division by cells in the population during these three days. As about 33 cells per ml were being lost each day from the surface of the snowpack in 1999 (section 4.4.1b) during fine weather, and the storm included particularly heavy rain, washout of cells from the snowpack was probably a major factor. Finally, snowfall during the last part of the storm implies that temperatures were below zero (see above). All these factors combined to give a period considerably less amenable to growth than the more sustained and wetter period of 1998.

According to Jones (1991), the inorganic nutrients in snow are readily bioavailable. The present results suggest a mechanism by which snow algae are effectively denied these nutrients until a combination of sufficient LWC and non-inhibitory light intensity become amenable for their utilisation. Storm events in which a large amount of rainwater is incorporated into snow are crucial for providing these conditions.

4.4.5 Summary

Much more snow was deposited on Mt Philistine during the winter of 1997 than 1998. As a consequence, melting of the tarn surface snow took longer to reach an advanced stage, and the bloom of snow algae was correspondingly later in the season. The degree of melting of the snowpack therefore appears to influence when *Chlainomonas kolii* appears in the spring.

Chlainomonas kolii is found in high numbers only in the surface tarn snow. Other snow algae are more common in other areas of the site, especially deeper in the snowpack. Therefore, different snow algae on the site have different ecological preferences.

Levels of NH_4-N, NO_3-N, and DRP in the Mt Philistine snow are generally lower than those found in Northern Hemisphere snowpacks. Water stress may also be more severe than in the well-studied forested snowpacks of North America, due to strong diurnal freeze-thaw cycles in the alpine zone. Very high light intensities during fine weather may be inhibitory to growth. Substantially lower snow algae cell abundances reflect the comparitively harsh conditions on Mt Philistine.

NH_4-N is the most abundant inorganic-N species in Mt Philistine snow. It was also the only nutrient which was detectably influenced by the algal population. DRP was not detectably utilised. NH_4-N is therefore the most important of the measured nutrients for the growth of *Chlainomonas kolii*.

Demonstration of preferential elution of nutrients from the bulk snow indicates that meltwater occupying the interstitial water spaces between snow crystals may contain much higher concentrations of nutrients than those found by analysis of bulk snow samples. This is a particularly important finding in the context of amenable growth conditions for algae, because growth occurs during major rainstorms when melting rate is at a maximum and the liquid water content (LWC) of the tarn snow increases dramatically. Additional favourable factors for growth during storms may be increased levels of NH_4-N in tarn snow interstitial water and decrease of light intensities to non-inhibitory levels.

Comparison of my results with the distribution of *Chlainomonas kolii* in North America suggests that the ecology of the organisms may be remarkably similar, despite growth in snowpacks which appear to be quite different.

CHAPTER 5.

DISPERSAL OF TERRESTRIAL AND SNOW ALGAE

5.1. Introduction

5.1.1. Airborne dispersal of algae

Algae which are most easily dispersed by wind are generally terrestrial, because small soil particles with which they are associated are easily lofted under dry conditions (Brown *et al.* 1964, Smith 1973, Marshall and Chalmers 1997). Gayley *et al.* (1989) found that spring maxima in diatom abundance in Greenland ice cores coincided with dust maxima. Cultivated soils are especially prolific sources of airborne algae, with dusty air reaching concentrations of up to 3000 algae m^{-3} (Brown *et al.* 1964).

Aeolian dispersal of freshwater algae occurs when lowering of water bodies exposes underlying sediments, and wind velocities are high enough to entrain cell-size particles (Gayley *et al.* 1989). These are essentially the same conditions required for dispersal of terrestrial algae. Marine algae may be lofted by droplet release from whitecaps, and by wind transport of foams and scums (Kristiansen 1996).

Wind transport of the snow alga *Chlamydomonas nivalis* has been suggested to occur (Kol 1942, Stein and Amundsen 1967, Mosser *et al.* 1977), and considerable numbers of cysts have been found in collectors on Signy Island, Antarctica (Marshall and Chalmers 1997). More snow algae cysts were found in aerobiota collectors in areas where there was less snow. Aerobiota collected at higher altitude sites contained fewer cysts, despite their abundance in surrounding snow. These sites had less exposed soil than lower sites. It seems likely that greater melting at lower sites deposited more cysts onto exposed rocks and soil, and only then did the cysts become available for transport.

This view corresponds to that of other authors. Fukushima (1963) believed that cysts were wind-transported only following deposition onto underlying substrata when snow melted. Cysts attached to plant surfaces following wind dispersal were suggested to inoculate the next season's snowcover. However, this mechanism could not explain the recurrence of coloured snow in regions lacking trees. Hoham (1971) exposed agar plates over a 72 hour period and found one dispersed cell. He believed that mass blooms could not be initiated by wind-dispersed spores. Recurring blooms in the same location every year are now generally thought to result from germination of the previous year's cysts underneath the subsequent snowcover and migration of flagellate daughter cells to the surface (e.g. Jones 1991, Thomas and Duval 1995). However, this could not explain the recurrence of non-motile forms such as *Raphidonema nivale*. Since

Raphidonema is thought to be a facultative cryophile, perhaps sourced from soil (Hoham 1973), there is still a possible case for aeolian inoculation of snow.

5.1.2. Environmental influences on dispersal

Most authors believe that dry conditions are important for dispersal (e.g. Strøm 1926, Brown *et al.* 1964, Gayley *et al.* 1989, Marshall and Chalmers 1997), although rainsplash has been implicated in lofting of cells (Rosas *et al.* 1989).

Meteorological conditions affect dispersal in other ways. A linear relationship has been found between concentration of airborne algae and vapour pressure and temperature of the air in Minatitlan, Mexico (Rosas *et al.* 1989) . In Mexico City, wind velocity was associated with variation in the algal count. Schlichting (1964) found more species in prevailing winds of 22-29 km hr^{-1} (with gusts to 55) than in winds of 51-56 km hr^{-1} (with gusts to 85). However, a very close correlation between mean wind speed and mean cell numbers has been found elsewhere (Smith 1973). Broady (1996) believed that more aerobiota should be found at higher wind speeds.

5.1.3. Ranges of dispersal

Colonisation of sterile environments by wind-dispersed algae is known to occur (e.g. Forest *et al.* 1959, Wynn-Williams 1993), but study of transport over long distances is complicated by difficulties in identifying sources of inoculum (Schlichting 1974) and ignorance about survivability of transported cells (Walton 1990). Wind-dispersal of diatom frustules is well-known, but viability of the cells is seldom reported (Kociolek and Spaulding 2000).

Surtsey Island, the result of a submarine volcanic eruption in the Atlantic Ocean, was found to be colonised by algae typical of Iceland which were presumably wind-dispersed (Kristiansen 1996). Antarctica is suggested to have been "made sterile" by glaciation during ice-ages (Walton 1990), and its algal flora has been regarded as containing "very few endemic species but a very large number of cosmopolitan ones" (Kristiansen 1996). However, it is likely that many refugia (nunataks, ice-shelf ponds) were present during ice ages, and there are still major gaps in knowledge of Antarctic non-marine algal floras. Some major ice-free areas which were overridden by glaciers have since been re-colonised, but propagules have probably been sourced from local refugia, although also possibly from other continents (Broady 1996). Evidence for the

latter includes South American pollen grains in snow, thermophilic algae present on fumarolic ground, and diatom frustules found in deep ice. Wind directions are also favourable for dispersal from other continents (Broady 1996).

Most wind-dispersed algae occur as saltating particles which can be detected only when collectors are placed within 10 cm of the ground (Hawes 1991). Saltating cells would clearly be unable to overcome large barriers such as oceans. However, algae have been detected in samples taken from aircraft at least 2000 m above the ground (van Overeem 1937, Brown *et al.* 1964).

The concept of cosmopolitanism in algal populations is problematic. For example, the name *Stephanodiscus astraea* (Ehrenberg) Grunow has been applied to at least 10 species of diatoms in 2 genera in published accounts (Kociolek and Spaulding 2000). These authors believed that widely accepted views concerning world-wide cosmopolitanism of diatoms are invalid, due to inaccuracies in identifications. Likewise, inadequacies of many identifications from Antarctica have been acknowledged, especially of morphologically simple algae such as small spheres (Broady 1996). Comparisons using molecular techniques have shown that species which are very similar morphologically may be evolutionarily distant, for example in the genus *Chlorella*, where *C. minutissima* Fott & Novakova and *C. kessleri* Fott & Novakova have been placed in the Trebouxiophyceae, while others such as *C. fusca* Shihira & Krauss remain in the Chlorophyceae (Booton *et al.* 1998). Endemism in algal populations may therefore be more difficult to detect than has previously been recognised. This may be an important consideration in studies of dispersal, where many common genera have been found in widely distant geographic locations (e.g. van Overeem 1937, Brown *et al.* 1964, Rosas *et al.* 1989).

5.1.4. Apparatus for collection of aerobiota

A range of aerobiota collectors exist, from ground-based to aeroplane mounted. They may be either passive, involving no motorised intake of air, or active, where a known air mass is mechanically sampled (Benninghoff 1992). Wynn-Williams (1992) recommended four alternatives in the absence of an ideal system (i.e. appropriate for all conditions and particle sizes). Two of these, the Tauber trap and the inverted Frisbee, are passive samplers which are described as non-quantitative. If the aim is to sample aerobiota from very local sources, the Frisbee will be more efficient, being closer to ground level (unless the Tauber trap can be buried), and it also has a wider aperture.

Particles of less than 50 μm diameter are less efficiently collected by Frisbees than are larger particles (Hall and Upton 1988).

The other two types of apparatus are active samplers, which process a known volume of air in a given time period. The rotorod sampler is a small electric motor driving upright H- or U-shaped wire arms, usually coated with an adhesive, which spin and collect particles. The jet spore sampler draws a known volume of air through a filter by suction. A major disadvantage of both techniques is their requirement for electrical power, meaning they cannot be left unattended for a long period, such as an extended storm when maximum dispersal of propagules would be expected (Hawes 1991), unless solar cells are available. Jet spore samplers and batteries are also very heavy, reducing ease of transport and possibility of replication.

Both rotorod and jet spore samplers have collected fewer particles in field trials than simple passive samplers (Benninghoff 1992). Hawes (1991) captured no culturable propagules on the McMurdo Ice Shelf, Antarctica, using jet spore samplers, but a considerable amount of material in Tauber traps. Probable reasons for this were the higher position of the aperture of the jet spore sampler, located above saltation level, and absence of the jet sampler during the strongest winds of the study period.

5.1.5. Aims

The extent of algal dispersal by wind on Mt Philistine is unknown, but the widespread distribution of many species at the site (Chapter 3) suggests that it may be an important process. This suggests the following objectives.

- To investigate transport by wind of snow algae cysts. Do they remain on the surface of substrata underlying the snow after melting? Are they present in aerobiota, and if so, when?
- To investigate which other algae are being dispersed. How readily are algae in Mt Philistine habitats lofted into the local aerobiota?
- To determine whether algae from elsewhere, which are not established on Mt Philistine, are being dispersed there.

5.2. Methods

5.2.1. Apparatus for collection of aerobiota

Inverted Frisbees were used to collect aerobiota, due to the advantages outlined in section 5.1.4 (Wynn-Williams 1992). A hole of approximately 2 cm diameter was drilled in the centre of each Frisbee. A polyethylene screw-cap was attached to the convex side of each Frisbee using a hot glue gun. Two plastic loops were attached adjacent to this in the same way. Nylon cord tied to these was used to secure the apparatus to the ground using rocks, taking care to minimise contamination. Where this was insufficiently secure, rocks rested against the edge of the Frisbee were used to prevent loss in strong winds (Fig. 5.2.1a, b, e).

5.2.2. Preparation, placement and sampling of apparatus

Frisbees were flame-sterilised in the laboratory using ethanol, then transported to the site in pairs taped together with sterile sides facing inwards. Each collector was rinsed with sterile water at the time of placement on site, and this water was kept for enumeration of any algal contaminants. Collectors were placed at ground level in order to catch saltating cells. Frisbees were set out on 28 October 1999.

Two replicate Frisbees were sited in each of the upper basin, middle basin, and top and bottom of lower basin (see Fig 5.2.1c, d and Chapter 2, Fig. 2.4 for exact locations).

Samples were taken from Frisbees by introducing up to 150 ml of sterile water into the collector (sometimes residual rainwater performed this function), swirling to distribute particles as evenly as possible, uncapping the central hole, and draining into a 200 ml sterile screw-top container. Care was taken to minimise contamination from surrounding moss-covered rocks. Samples were then frozen at -15°C until analysis. Sampling dates were 13 and 26 November, 9 and 26 December 1999, and 13 January 2000 (15, 13, 13, 17 and 18 day intervals between sampling respectively).

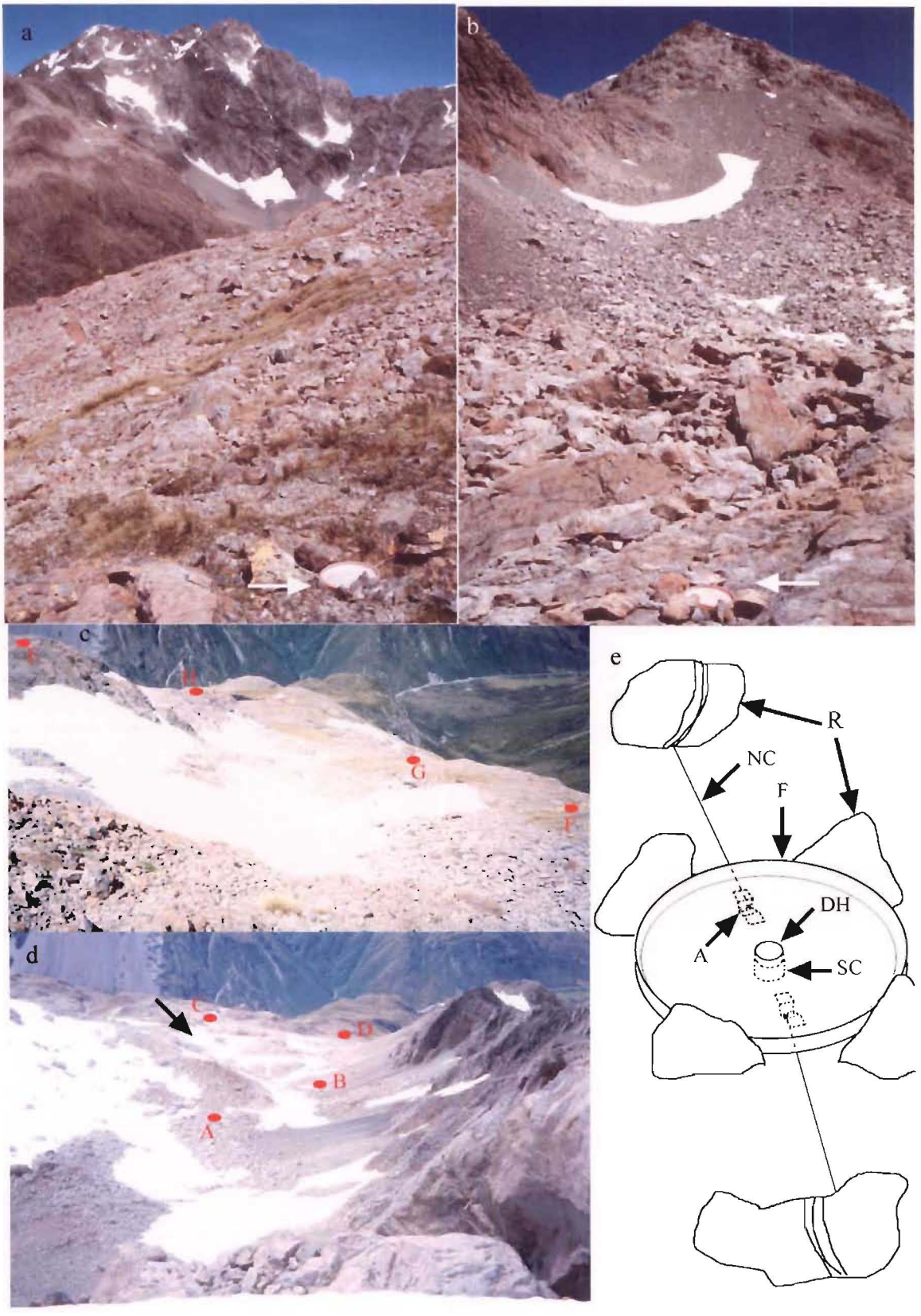


Fig. 5.2.1. Aerobiota collection, 1999: a, Frisbee F (arrow), Mt Rolleston in background; b, Frisbee A (arrow), top of Mt Philistine (1965m) in background; c, lower basin viewed from site of Frisbee D on edge of middle basin, showing Frisbee locations (E, F = top of lower basin, G, H = bottom of low basin); d, upper and middle basins from summit of Mt Philistine showing Frisbee locations (A, B = upper basin, C, D = middle basin, arrow indicates tarn site); e, diagram showing placement of Frisbee collector (F = Frisbee surrounded by rocks, NC = nylon cord, A = attachment point, DH = drainage hole, SC = screw cap, R=rocks arranged to hold down Frisbee). Frisbee labels correspond to those in Chapter 2. Photos a, b taken 13 January 2000, c taken November 1998, d taken November 1999.

5.2.3. Removal of snow samples for analysis of aerobiota

Algae deposited on snow were sampled on 13 and 26 November and 9 December from as close as possible to locations of Frisbees in the upper basin, middle basin, and top of the lower basin. Snow surface samples were removed directly into 200 ml sterile screw-cap polycarbonate containers and frozen until analysis.

5.2.4. Preparation of samples from Frisbees and snow

Samples in the 200 ml containers were melted and concentrated by sedimentation for approximately 48 hours. Most of the water was removed, and the remainder resuspended and poured into 10 ml polycarbonate screw-cap test tubes. These were concentrated further by sedimentation for 24 hours, and approximately half the water was removed. For snow samples, which were treated quantitatively, the weight of the sample at each stage, and the empty weight of each container and tube, were recorded to allow accurate calculation of final concentration factors. This allowed calculation of cell numbers in each snow sample.

5.2.5. Enumeration of viable aerobiota by culture counts

Culture plates for enumeration of algae in Frisbee and snow samples were made as described in section 3.2.3c. Additionally, surfaces of solidified medium were dried in an oven at 60°C for 30-40 minutes to remove excess water and allow absorption of inoculum. Inoculation and culture were as described in section 3.2.3c.

Cultures were grown for three weeks before making counts of each colony type under a dissector microscope at 40x. The algae were identified by examining one of each colony type per plate by light microscopy at magnifications up to 1000x. Algae were grouped by colony type in results, because not all colonies of each type could be examined, and different algae could give rise to the same type of colony.

After inoculation of cultures, a drop of Lugol's iodine was added to each remaining concentrated sample to preserve them for direct counts.

5.2.6. Enumeration of aerobiota by direct microscopic counts

Modified Palmer-Maloney type chambers manufactured in the laboratory (see Chapter 4) were used for direct counts. Each counting was continued until either 100 cells of the dominant type from each suspension had been counted or 4 chambers had been examined. Results for each species were expressed as proportions of the total count for each sample on each occasion (i.e. as relative counts).

Counts of *Nothofagus* pollen in Frisbee samples were used to standardise relative counts of algae from Frisbee samples, so that spatial and temporal comparisons could be made. Validity of this procedure was assessed by determining spatial and temporal variability of pollen counts from snow samples. Standardisation by pollen count was done on data from only the first three sampling occasions, when conservation of pollen counts between sites and times could be demonstrated from counts in snow. Identification of pollen was made according to Moar (1993).

5.2.7. Statistical analyses

Means of direct counts from snow samples and standardised direct and plate counts from Frisbee samples were analysed for significant differences using analysis of variance (Anova) on the statistical computing package S-Plus 2000 (Mathsoft 1999). Homogeneity of variance was assessed by fitting the Anova models and then plotting fitted values against residuals and visually inspecting the graph. Where necessary, data was log-transformed to achieve homogeneous variance.

Statistical tests were not performed on relative cell count data from Frisbee samples because the number of cells counted in calculating each proportion was highly variable.

5.3. Results

5.3.1. Algae dispersed onto snow

Fischerella sp. and cf. *Gloeocapsa* dominated the non-snow algae deposited onto snow (Fig. 5.3.1). Very few chlorophytes, diatoms, or xanthophyceans were found. Accumulation of algae in surface snow over the time period studied was not

Table 5.3.1. Numbers of non-snow algae grown from snow samples taken during 1999 study period on Mt Philistine.

Algae	Number of colonies on plates								
	13 November			26 November			9 December		
	U[1]	M[2]	L[3]	U[1]	M[2]	L[3]	U[1]	M[2]	L[3]
cf. *Gloeocapsa*[4]	0	0	2	3	0	0	0	0	0
Myrmecia cf. *biatorellae*	0	0	1	2	0	0	0	0	0
Myrmecia cf. *irregularis*	0	0	0	1	0	0	0	0	12
Chloromonas sp	0	0	0	0	0	0	0	0	1
Oocystis cf. *minuta*	0	0	0	1	0	0	0	0	0

[1] Upper Basin.
[2] Middle Basin.
[3] Top of Low Basin.
[4] Counted only when producing colourless mucilage.

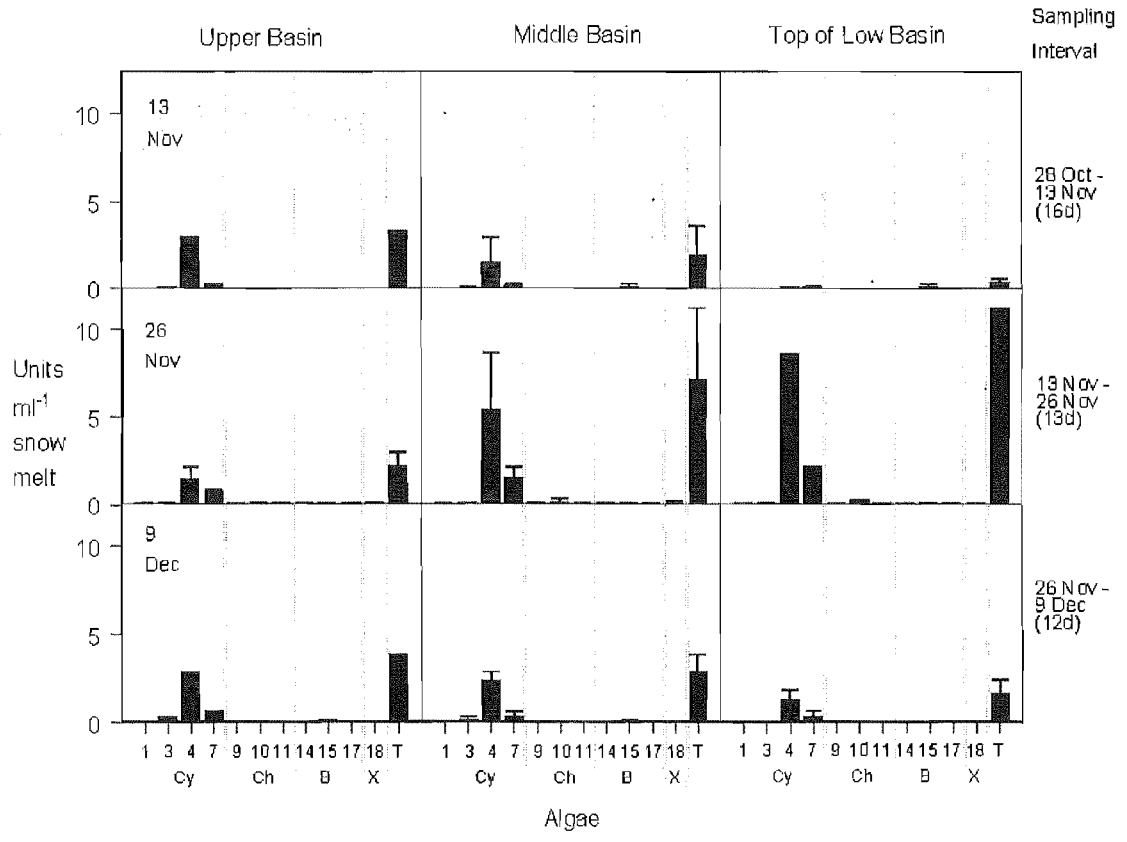


Fig. 5.3.1. Direct counts of algae dispersed onto snow on three sampling occasions, 1999 study period. Replicated data are means of 2 samples per basin ±1SE. Data without error bars are unreplicated. Key to Algae: Cy=Cyanophyta, 1=cf. *Ammatoidea*, 3=*Cyanothece aeruginosa*, 4=cf. *Gloeocapsa*, 7=*Fischerella* sp., Ch=Chlorophyta, 9=*Klebsormidium flaccidum*, 10=snow algae cyst (possibly *Chlamydomonas*), 11=unidentified green unicells, B=Bacillariophyceae, 14=*Cymbella kapii*, 15=*Gomphonema parvulum* + *Navicula* sp., 17=*Gomphonema truncatum*, X=Xanthophyceae, 18=Xanthophyceae sp. 1, T=total algae. Sampling date is at left hand end of each row.

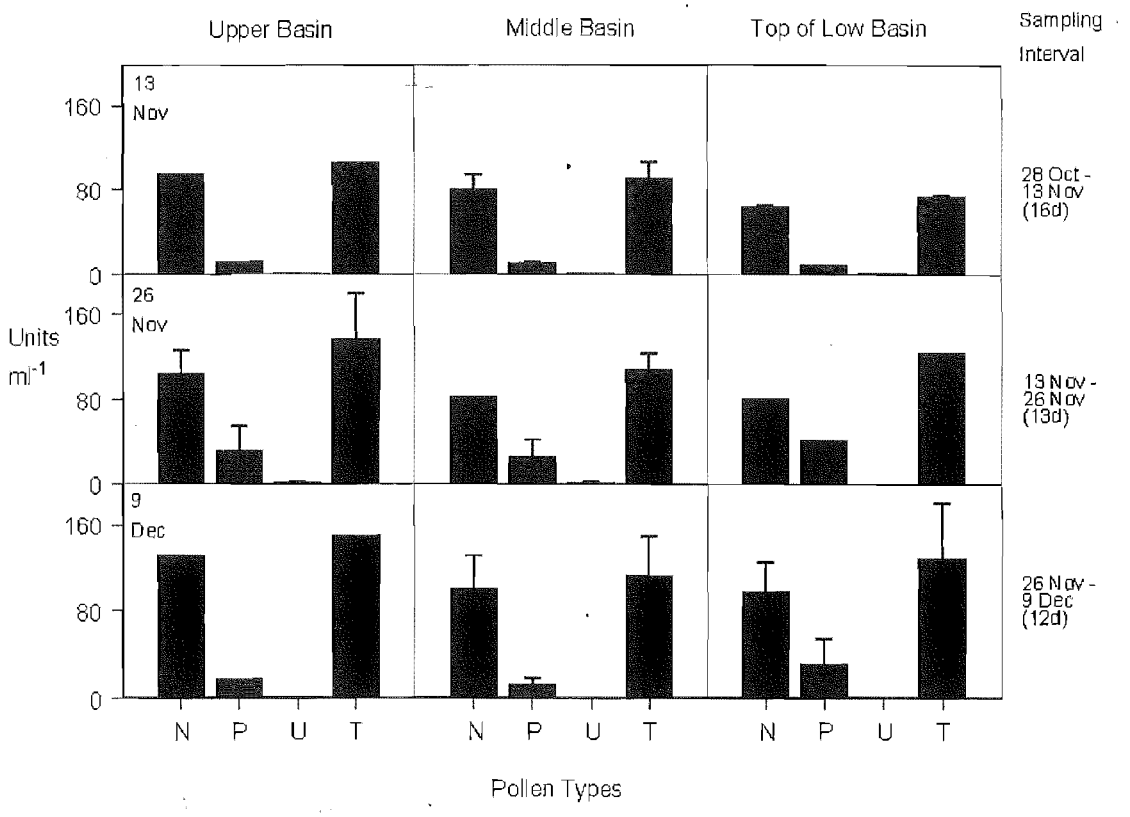


Fig. 5.3.2. Pollen counts from snow samples taken on three occasions during 1999 study period. Replicated data are means of two samples per basin ±1SE. Data without error bars are unreplicated. Key to pollen types: N = *Nothofagus* pollen, P = pine pollen, U = rare unknown pollen type, T = total pollen.

Table 5.3.2. Counts of algae and pollen from wash samples of Frisbee collectors, taken 28 October 1999.

Location of Frisbee[1]	Replicate	Algae (direct count)[2]	Pollen (direct count)[2]	Algal colonies on agarised culture plates
Upper basin	1	4	2	0
	2	3	2	0
Middle basin	1	1	2	0
	2	2	3	0
Low basin (top)	1	0	6	0
	2	0	7	0
Low basin (bottom)	1	0	0	0
	2	NA	NA	NA

[1] Refer to Chapter 2, Fig. 2.4 for precise locations.
[2] Total volume of sample examined = 0.28ml in 4 replicate counting chambers.
NA = sample lost.

detectable. Numbers of algae found in snow in different basins were significantly different (Anova, P=0.007), due to lower numbers found in the upper basin than in the middle and lower basins (Fig. 5.3.1; t-Tests, P=0.039, 0.003). Further analysis was

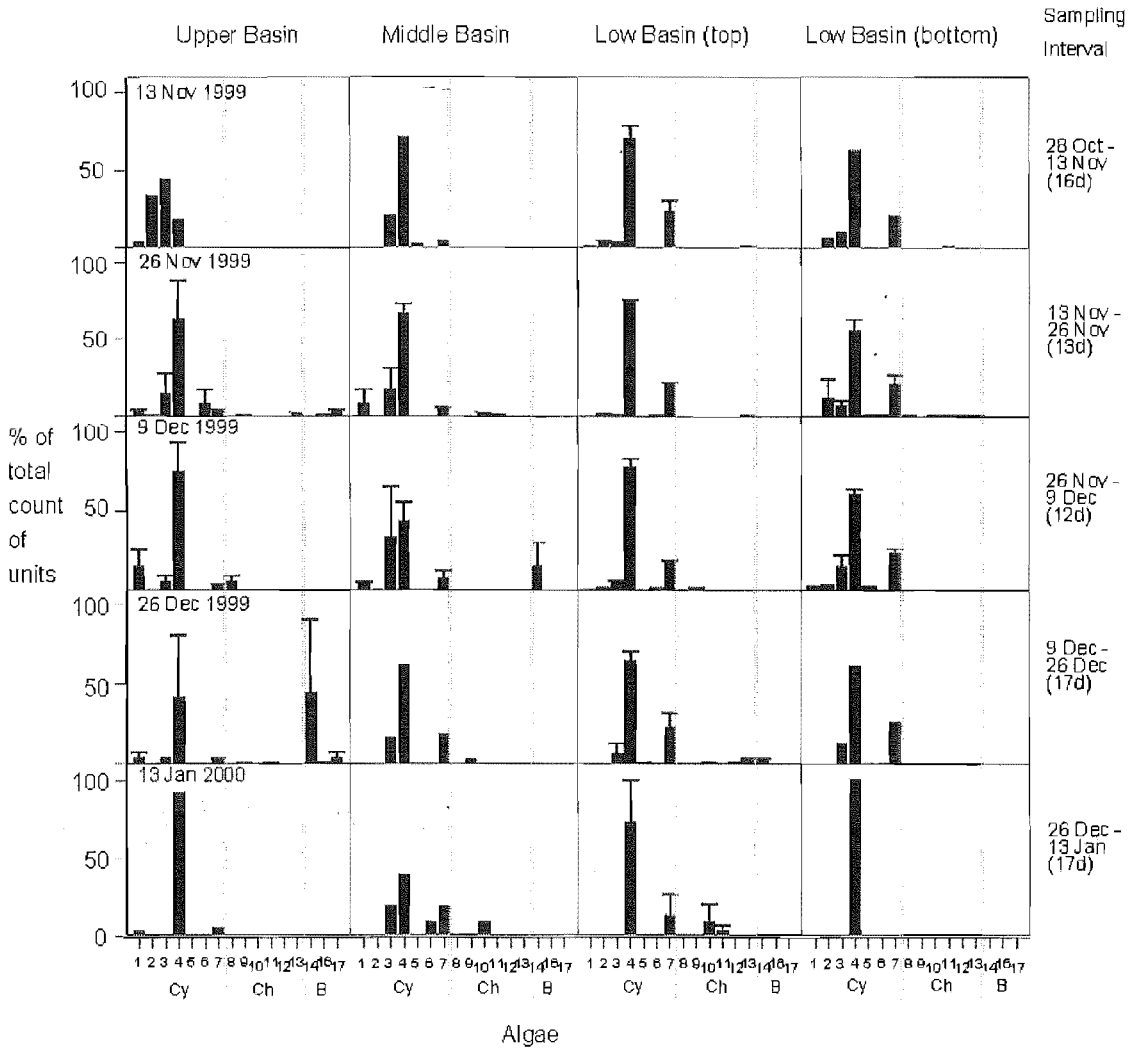


Fig. 5.3.3. Relative numbers of algae present in Frisbee collectors on five dates during summer 1999-2000. Replicated data are means of two samples per basin ±1SE. Data without error bars are unreplicated. Key to Algae: Cy=Cyanophyta, 1=cf. *Ammatoidea*, 2=*Chroococcus* sp., 3=*Cyanothece aeruginosa*, 4=cf. *Gloeocapsa*, 5=*Hormoscilla* sp., 6=*Phormidium* cf. *retzii*, 7=*Fischerella* sp., Ch=Chlorophyta, 8=*Klebsormidium elegans*, 9=*Klebsormidium flaccidum*, 10=snow algae cyst (possibly *Chlamydomonas*), 11=unidentified green unicells, 12=Zygnemataceae sp. 1, 13=Desmids (mainly *Cylindrocystis*), B=Bacillariophyceae, 14=*Cymbella kapii*, 16=*Synedra ulna* var. *contracta*, 17=*Gomphonema truncatum*, X=Xanthophyceae, 18=Xanthophyceae sp. 1, T=total algae.

hampered by insufficient replication to compare individual basins at different times, but the source of significance is probably due to 26 November results.

Very few algae grew in cultures (Table 5.3.1).

5.3.2. Pollen dispersed onto snow

Nothofagus was the most abundant type of pollen found in Mt Philistine snow (Fig. 5.3.2). Pine pollen and a rare unidentified type were present in lower numbers. There was no effect of location or time on pollen counts from snow (Anova, P=0.70,

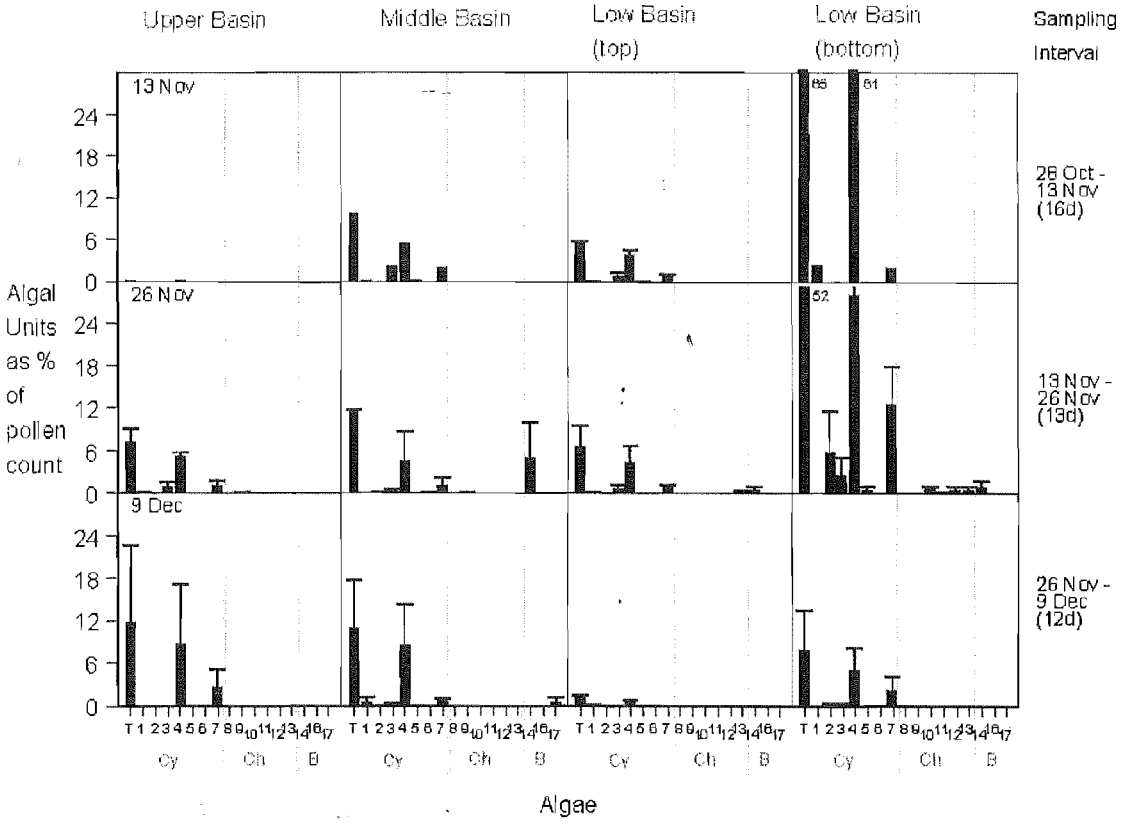


Fig. 5.3.4. Data for first three days of Fig. 5.3.3 expressed as % of pollen counts. Replicated data are means of two samples per basin ± 1SE. Data without error bars are unreplicated. Key to Algae: see Fig. 5.3.3. Lower basin (bottom) samples on 13 and 26 November are contaminated with *Andreaea* moss. Sampling date is in top left hand corner of each row.

0.28). As observed for algae, no accumulation of pollen in snow occurred over the duration of the study.

5.3.3. Algae dispersed into Frisbee collectors

a. Testing for contamination. No algal colonies grew from wash samples taken from Frisbees at time of placement, 28 October (Table 5.3.2). Very low numbers of algae and pollen were observed in direct counts from the washes, presumably captured before or during washing (the collectors were set out during a north-westerly storm).

b. Enumeration of aerobiota by direct microscopic counts. Cyanophyta dominated in abundance and species richness. The highest proportion of the total count was always attained by cf. *Gloeocapsa* (Fig. 5.3.3), except on 26 December in the upper basin when *Cymbella kapii* reached similar numbers, and 9 December in the middle basin when *Cyanothece* was found in high numbers. Chlorophytes were seldom

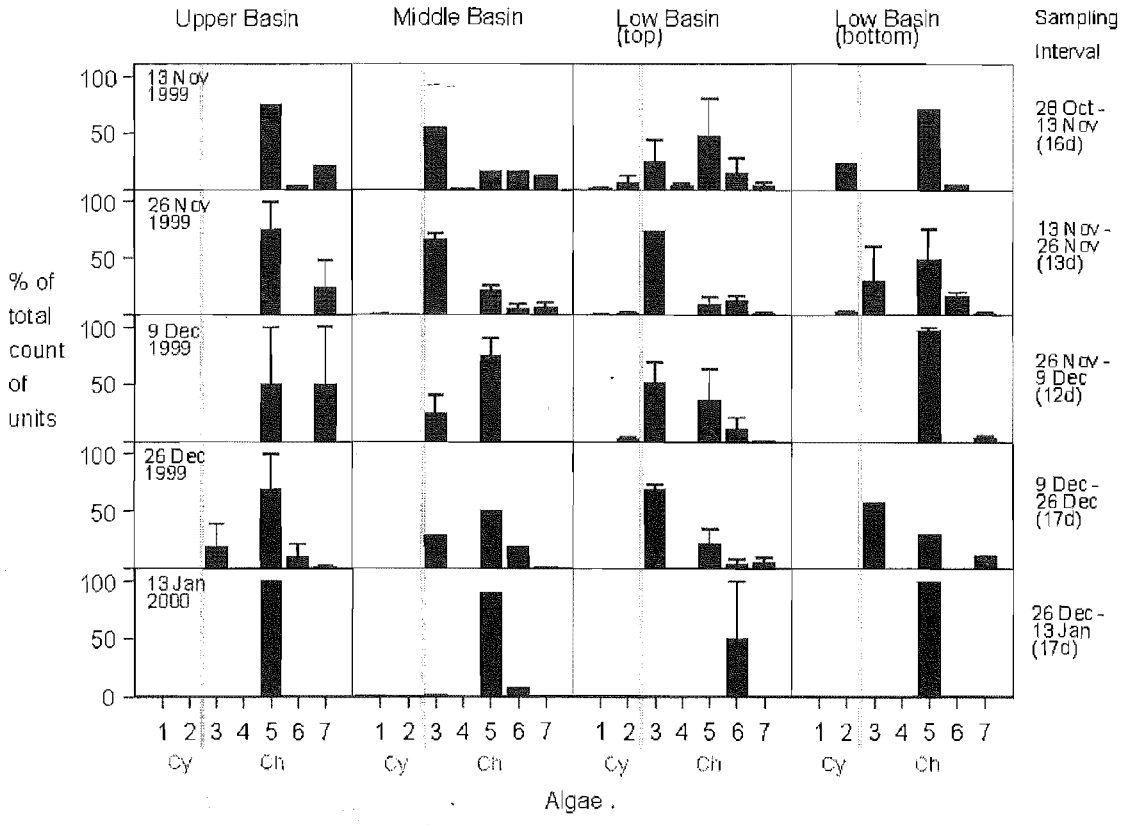


Fig. 5.3.5. Relative numbers of algal colonies grown on agar plates inoculated with Frisbee samples from different basins and different occasions, summer 1999-2000. Data are means for two samples, each with two replicate plates, ±1SE. Data without error bars are unreplicated samples with two replicate plates. Key to Algae: Cy=Cyanophyta, 1=*Phormidium* cf. *retzii*, 2=cf. *Gloeocapsa*; Ch=Chlorophyta, 3=*Pseudococcomyxa simplex* + *Stichococcus* cf. *bacillaris*, 4=*Stichococcus* cf. *mirabilis* + *Microthamnion strictissimum*, 5=*Myrmecia* cf. *irregularis* + *Oocystis* cf. *minuta* + *Elliptochloris* cf. *reniformis* + *Chlorella* cf. *homosphaera* + *Myrmecia* cf. *biatorellae* + *Chlorococcum* cf. *tatrense*, 6=*Coccomyxa gloeobotrydiformis* + *Gloeocystis papuana* + *Chlamydocapsa* cf. sp. + *Chlamydomonas* sp. + *Chloromonas* sp., 7=*Klebsormidium* cf. *flaccidum*. Sampling date is in top left hand corner of each row.

recorded. Diatoms were very sporadically distributed, exceeding 10% on only two occasions (9 and 26 December in middle and upper basins respectively) but were seldom recorded at other times. No xanthophyceans were observed.

Snow algae cysts (possibly *Chlamydomonas*, as shown by Marchant 1982) were very infrequent, and were present in collections from only the middle basin and top of the lower basin.

One Frisbee collector in the lower basin was contaminated with moss by accidental scraping of anchoring rocks during sample extraction on 13 and 26 November. This was evident when data was expressed quantitatively as % of pollen counts (Fig. 5.3.4). There was no significant difference in algal numbers in Frisbees between different sampling intervals or basins when this data was omitted from the analysis (Anova, P=0.25, 0.28). There was considerably more pollen than algae

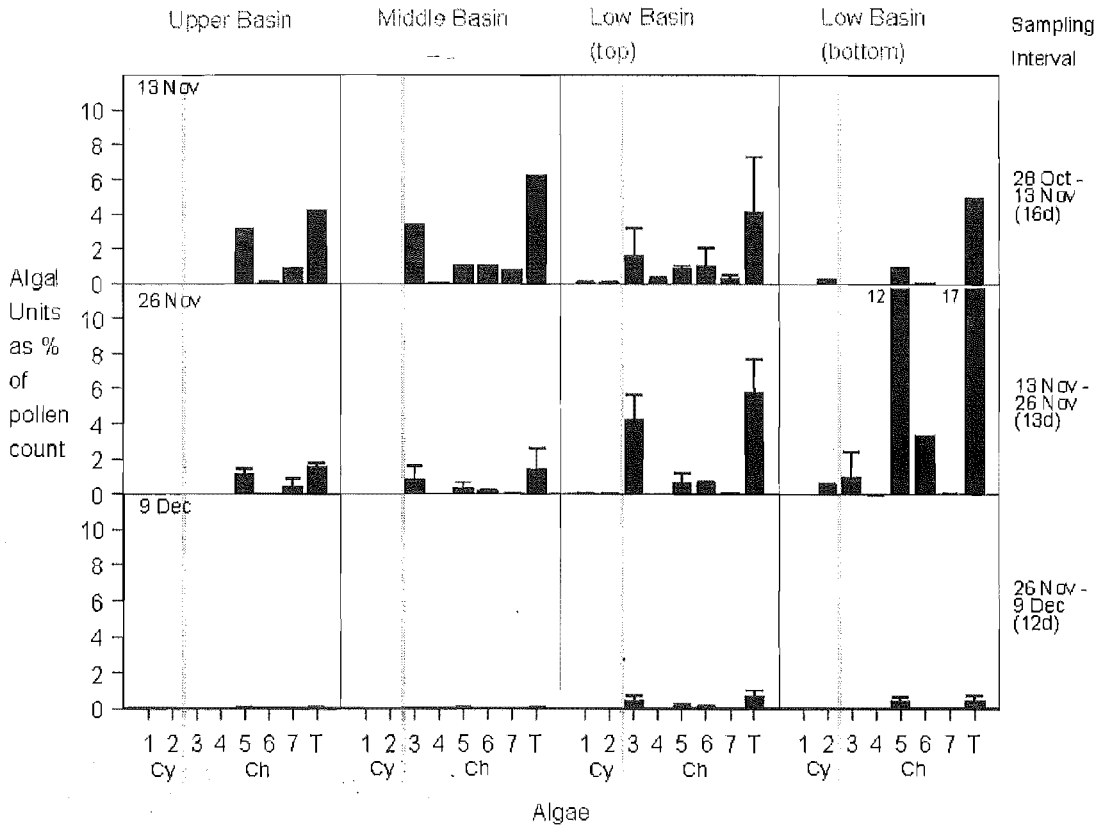


Fig. 5.3.6. Numbers of algal colonies on culture plates from first three sampling intervals expressed as % of pollen counts. Data are means for two samples, each with two replicate plates, ±1SE. Data without error bars are unreplicated samples with two replicate plates. Key to Algae: see Fig. 5.3.5, T=total algae.

dispersed into Frisbees, as uncontaminated collectors recorded a maximum algal count of 11±7% of the pollen count.

c. Enumeration of viable aerobiota by culture counts. Plate counts were dominated by chlorophytes. Spherical to near-spherical chlorophyte unicells (*Myrmecia* cf. *irregularis*, *M.* cf. *biatorellae*, *Chlorococcum* cf. *tatrense*, *Oocystis* cf. *minuta*, *Elliptochloris* cf. *reniformis*, and *Chlorella* cf. *homosphaera*), were usually dominant (Fig. 5.3.5). Occasionally elongate-pyriform to straight cylindrical unicells (*Pseudococcomyxa simplex* and *Stichococcus* cf. *bacillaris*) were dominant, but never in the upper basin. Mucilaginous colonial forms (*Coccomyxa gloeobotrydiformis*, *Gloeocystis papuana*, and palmelloid *Chloromonas* and *Chlamydomonas* species) dominated on one occasion (13 January, top of low basin).

Of the algae which were detected in both direct and plate counts, *Klebsormidium* cf. *flaccidum* was found most frequently on plates. Cf. *Gloeocapsa*, which dominated

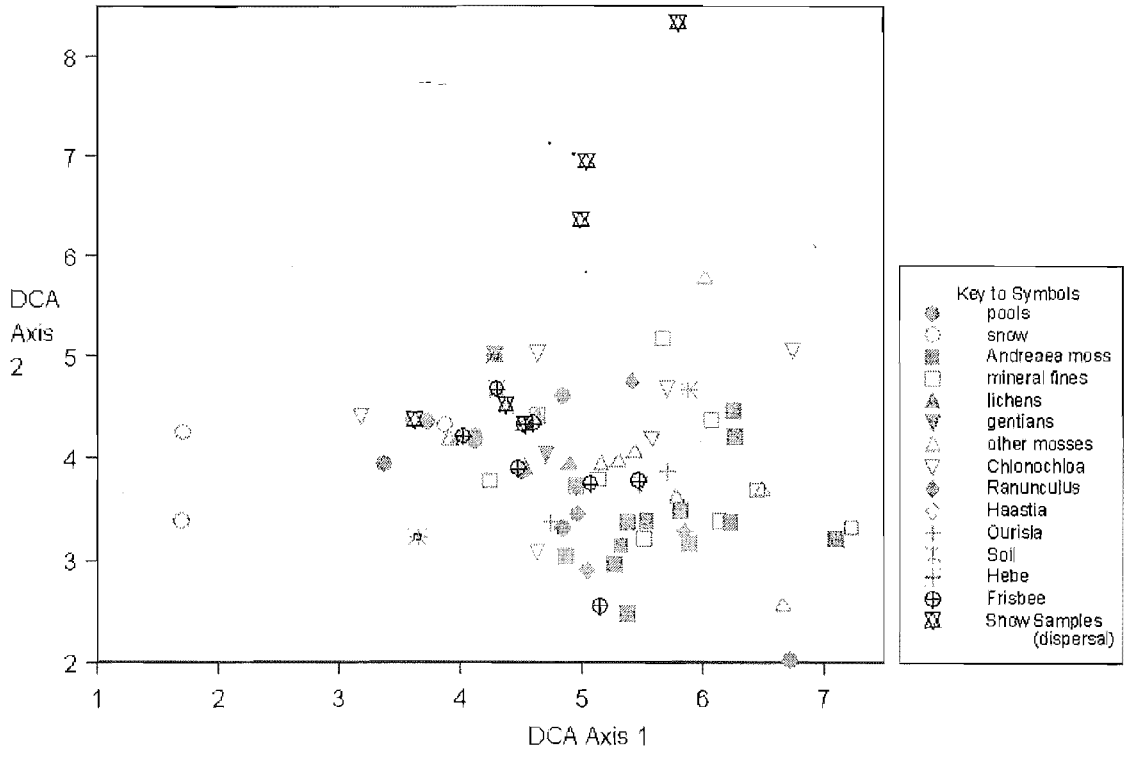


Fig. 5.3.7. Detrended Correspondence Analysis results for distribution data set used in Chapter 3 (results from direct examination only), incorporating scores from Frisbee collector samples and snow samples used in dispersal analysis. All samples were collected 9 December 1999.

direct counts, was found in a clearly living state (i.e. producing new mucilage) only on plates from low basin samples.

The effect of contamination on numbers of algae in the bottom low basin samples is not detectable on 13 November when numbers are expressed as % pollen count (Fig. 5.3.6). Contamination was detectable in these samples on 26 November, in which a high level of type 3 colonies (spherical green unicells, see caption Fig. 5.3.5) were found. The total numbers of algae expressed as % pollen count, with the contaminated samples from 26 November removed, were significantly different on different sampling days (Anova, P=0.005). Algal numbers were higher on both 13 and 26 November than on 9 December (t-Tests, P=0.032, 0.002). Numbers of culturable algae in Frisbee collectors were not significantly different in different basins (ANOVA, P=0.207).

Several Frisbee collectors were lost during the study period, which is shown by lack of replication in some of the results. All but one were subsequently recovered and

replaced. Most were blown down the site by very strong winds; at least one was removed by a tramper and others may have been tampered with by kea (see Chapter 2).

5.3.4. Comparison of species composition in aerobiota samples with habitat samples

Frisbee samples grouped centrally in the ordination diagram when combined with distribution data from 9 December 1999 and used in a DCA (Fig. 5.3.7). Results from cultures were omitted from this analysis because the viable algal counts were grouped according to cell morphology (see section 5.2.5), whereas they were scored as individual species in the distribution study (see section 3.2), so they were not easily comparable.

5.4. Discussion

5.4.1. Validity of Frisbee sampling

Samples testing for contamination on 28 October 1999 showed very low numbers of cells (Table 5.3.2). These were probably picked up on-site, as Frisbees were set out during stormy conditions with strong winds and rain.

Conserved pollen counts in snow between different basins and times (Fig. 5.3.2) justified their use to standardise results between different Frisbees. Unlike Brown *et al.* (1964), I found that abundance of pollen dispersed to the site was always much higher than that of algae (see vertical axes, Fig. 5.3.4, 5.3.6). Although still not a quantitative measure, the count data standardised by pollen can be compared between Frisbees and different sampling occasions. Comparison of standardised data between contaminated and non-contaminated samples confirmed that the technique was appropriate (Fig. 5.3.4). The moss contamination could not be visualised using non-standardised data (Fig. 5.3.3).

The species compositions of Frisbee samples on 9 December, the same day that samples for study of distribution were taken, fall within the central region of a combined ordination (Fig. 5.3.7). Therefore the samples collected in Frisbees seem

representative of many habitats on the mountain in terms of their species composition as detected by direct microscopic examination.

5.4.2. Dispersal of snow algae

Few snow algae cells were detected in Frisbee collectors (Fig. 5.3.3, 5.3.4). All those observed were red spherical cysts, probably not *Chlainomonas kolii* which dominates red snow blooms on the Mt Philistine tarn. Most were coated with mineral particles and appeared similar to those found in Kosciusko National Park, Australia (Marchant 1982). They have been found in low numbers in snowfields and other habitats throughout the Mt Philistine site (Fig. 3.3.7) and extensively in Mt Cook National Park. None to low numbers were collected in Frisbees in all cases including the middle basin where the tarn bloom occurs (Fig. 5.3.3, 5.3.4).

These observations appear to fit the prevailing explanation for occurrence of snow algae blooms in the same location year after year. It is thought that germination of the previous season's cysts beneath the snow gives rise to many zoospores which migrate to the surface through interstitial meltwater between the crystals (e.g. Jones 1991), wind-dispersed propagules not being important for bloom initiation (Hoham 1971). There is substantial evidence for this explanation from studies of tree-covered North American snow algae populations (Hoham 1971, 1975, Hoham and Mullet 1977, Hoham *et al.* 1979, 1983).

However, contradictory evidence from Mt Philistine has been found, raising questions about the relevance of this explanation to a New Zealand alpine setting. Firstly, substantial ice layers have been found, usually below about 30 cm depth, in all snowfields, including tarn and other snow, with and without snow algae present. An algal cell could not swim through these obstacles. Secondly, no snow algae cells of any type, except a single cyst of *Chloromonas* sp. 3 (see Chapter 6), were found in tarn sediment samples beneath the area where blooms occur, or any other sediment samples collected from the tarn bottom and shores on 26 December 1999. Thirdly, aggregations of snow algae were found floating in a scum on the tarn surface in December 1998, suggesting that these cells do not sink to the bottom of the tarn.

The Frisbee at the tarn site was lost sometime between 9 and 26 December (this is why the middle basin sample on the latter date is unreplicated). During this time the snow completely melted from the tarn, which is presumably when most cells were

released into the water and deposited on the leeward edge. Therefore it is possible that the bulk of dispersed cells were not sampled during the study.

It has been suggested that mass blooms of snow algae could not be initiated by wind-dispersed cysts (Hoham 1971). Perhaps initiation of the bloom by wind dispersal explains the much lower cell concentrations in Mt Philistine tarn snow blooms (1175 cells per ml maximum) compared to previous studies (typically greater than 10^5 cells per ml, see section 4.4.1). However, there is still no direct evidence for air-borne dispersal of *Chlainomonas kolii*. Further research is required to understand population development of this enigmatic organism.

It is likely that cells cannot be lofted directly from snowfields, but only when they have been deposited onto substrata by melting snow and then dried, in the same way as other aquatic algae (Strøm 1926, Brown *et al.* 1964, Gayley *et al.* 1989, Marshall and Chalmers 1997). This process has been observed on Mt Philistine, although not for *Chlainomonas kolii* (Table 3.3.2). Meltwater must carry some cells into cracks between rocks, especially in the upper and middle basins where large boulders underlie the snow (see Chapter 2). More are probably washed there by rain. Therefore, not all cysts in snow would be available for wind transport. Perhaps this is related to the generally low numbers of cysts found in snowfields apart from the tarn site.

5.4.3. Relating dispersal to distribution patterns

Algae were found blown onto snow in greater abundance in the middle and low basins than in the upper basin on 26 November (Fig. 5.3.1). This may be because the middle and low basins contain more amenable growth environments, being at a lower, more sheltered altitude which enables greater colonisation by mosses and higher plants (Chapter 2) which provide habitats for algae (Chapter 3). However, no climate data is available to support this suggestion.

Wind-dispersed cyanophytes were dominant in snow samples (Fig. 5.3.1), and usually also in direct counts from Frisbee samples (Fig. 5.3.3). Low numbers of cf. *Gloeocapsa* and *Phormidium* cf. *retzii* appeared in cultures made from Frisbee samples, but never from the upper basin. In contrast, chlorophytes were dominant in cultures (Fig. 5.3.5). They comprised low proportions of the total direct count from Frisbees and were virtually absent in these counts from 13 November samples. Chlorophytes were

rare in snow samples (Fig. 5.3.1, Table 5.3.1). Dispersal patterns of cyanophytes and chlorophytes from direct counts were fairly consistent throughout the study period.

All aerobiota recorded, except the diatoms, had previously been observed in habitat samples from the site. Algae most commonly found in direct examination of these samples are cf. *Gloeocapsa*, *Fischerella* sp. and *Cyanothece aeruginosa*, which group together in a species-by-sites ordination (see Chapter 3). The former two, and especially cf. *Gloeocapsa*, were also dominant in direct counts from Frisbee samples (Fig. 5.3.3, 5.3.4). The low occurrence of *C. aeruginosa* in collectors could be due to its occurrence primarily as single cells, whereas cf. *Gloeocapsa* and *Fischerella* sp. were collected in multicellular colonies and filaments respectively. Frisbees are known to be less efficient collectors of particles less than 50 μm in diameter (Hall and Upton 1988, Wynn-Williams 1992). Dominance in aerobiota of locally dominant algae is in accord with previous results (Forest *et al.* 1959, Broady 1979c, Hawes 1991).

Other cells often found in direct examination of habitat samples but infrequently in Frisbee samples include the desmids. Detection of these may be limited by their small size (maximum diameter 26μm), as reasoned for *Cyanothece*. Strøm (1926) suggested that vegetative cells of desmids could not be viable components of aerobiota due to loss of viability on desiccation, which could explain their low numbers in the aerobiota on Mt Philistine. Non-viable cells, especially those of *Mesotaenium* spp., could have been transported into Frisbees but not recognised when examined, if their cell contents were absent or unpigmented. Zygospores might be expected to survive desiccation, but none have been observed on Mt Philistine and, in general, they are rarely produced (Kristiansen 1996).

The common culturable algae previously isolated from Mt Philistine (see Chapter 3) also dominated the culturable algae in Frisbee samples. Unicellular algae comprised the highest proportion (Fig. 5.3.5, 5.3.6). *Klebsormidium* cf. *flaccidum*, a culturable filamentous alga isolated from a range of habitats on Mt Philistine, was observed less frequently (Fig. 5.3.6). Although this appears to contradict the conclusions drawn from the low numbers of *Cyanothece aeruginosa* in direct counts, it is likely that unicellular green algae were dispersed attached to larger soil particles and plant fragments. These algae have frequently been isolated from soil and plant samples (see Chapter 3), and low basin Frisbees always contained visible fragments of moss and vascular plants when sampled.

Plant material as an origin for many wind-dispersed algae is also suggested by the effect of accidental contamination of a lower basin Frisbee with *Andreaea* moss on

13 and 26 November (Fig. 5.3.4). This dramatically increased numbers of cf. *Gloeocapsa* and *Fischerella* sp., and also culturable algae in 26 November samples. Attachment of wind-dispersed algae to moss and lichen fragments on Signy Island, Antarctica, has been noted (Broady 1979).

Diatoms had a more sporadic pattern of dispersal than other types of algae. They were generally detected in very low numbers except on 9 and 26 December, when they reached 14% and 45% of the total Frisbee direct count respectively in the upper and middle basins. *Cymbella kapii* and *Gomphonema truncatum* have been recorded from freshwater habitats elsewhere in New Zealand, but not from Mt Philistine, and it is likely that their presence in Mt Philistine snow demonstrates transport of propagules from sources distant from the site. Cf. *Achnanthes* and *Stauroneis* cf. *prominula*, which are known to grow on site, were never detected as aerobiota. On 26 December in the upper basin, *Cymbella kapii* attained a high proportion of the total Frisbee count (Fig. 5.3.3). This shows that dispersal of propagules can be patchy and associated with unique transport events.

5.4.4. Comparison of dispersal of algae detected by direct examination and culturing

Algae detected by direct examination and those detected by cultures form two groups of organisms which are almost mutually exclusive. The three algae belonging to both groups are *Phormidium* cf. *retzii*, cf. *Gloeocapsa* (which, although it did not grow in culture, did indicate its viability by producing copious colourless mucilage) and *Klebsormidium* cf. *flaccidum*. The dispersal characteristics of the two groups will be discussed in this section, so for clarity it is important to define their general characteristics as clearly as possible.

Group A comprises organisms found in direct microscopic examination of sample material, but did not grow in agarised BG-11 cultures. They are mainly cyanophytes, which are probably relatively slow-growing on the site, and are "k" strategists which invest in large biomass at the expense of rapid growth rates.

Group B consists of organisms which are not, or very rarely, visible under direct microscopic examination of sample material. They grow rapidly in BG-11 cultures, and are "r" strategists which rely on rapid reproduction to achieve large populations quickly under favourable conditions. There is more confusion over their exact distribution than

for group A organisms due to probable culturing of propagules which are not always active components of the communities from which they were collected (see Chapter 3).

Temporal variation has been observed in the dispersal of group B, but not group A, algae into Frisbees (Fig. 5.3.4, 5.3.6). There are at least two possible explanations for this observation.

Firstly, the two groups may have differing growth periods on the site. Growth of group B organisms in culture demonstrates the ability of B, but not of A, to rapidly utilise relatively nutrient-rich resources. It has already been shown that initial snow-melt is more nutrient-rich than bulk snow (Table 4.3.4, Chapter 4), and that a large proportion of nutrients are released in spring melt (Section 4.1.6). Perhaps the higher abundance of group B in the aerobiota between 28 October and 26 November than between 26 November and 9 December is due to dispersal of populations growing on snowmelt. When snow disappears, such populations may cease growth, with a resultant depletion in cells available for dispersal.

Secondly, the two groups of algae may have different geographic sources of propagules. If this was the case, the source of propagules for group A was not affected between 26 November and 9 December, but the source of propagules for group B was. What different sources could explain this result? If group A had a local source (i.e. organisms growing on the site) and group B a distant source, weather patterns which might affect long-distance dispersal of B may not affect short-distance dispersal of A. There is evidence against this explanation: diatoms which are apparently sourced from elsewhere (see section 5.4.3) have a patchy distribution (Fig. 5.3.3), not approximately uniform as found for most of the group B organisms (Fig. 5.3.5).

Another possibility is different geographical sources of propagules of the two groups from within the study site. *Andreaea* moss appears to have a distinct flora, including an unusually high proportion of cyanophytes (Fig. 3.3.6). This is also a habitat which is distributed throughout the site, and is readily dispersed due to the easily fragmented nature of *Andreaea* moss when dry. Many group B organisms, such as *Stichococcus* cf. *bacillaris* and *Pseudococcomyxa simplex*, are chlorophytes which tend to associate with vascular plants and lichens (Table 3.3.2). These habitats are mostly found in the low basin (Table 3.3.1). Therefore, greater exposure and wind speeds in the upper basin could give rise to a continual rain of propagules from *Andreaea* moss, whereas dispersal of populations sourced mainly from the lower basin could fluctuate more as a result of the weather. Problems with this suggestion include an absence of data to show that windspeeds are higher in the upper basin, and that it has not been

found that many group B organisms have closely related geographic distributions (Fig. 3.3.12 – 3.3.14).

Weight of evidence available must favour the first explanation. The main problem lies in identifying the source of propagules, and obtaining an accurate understanding of distribution of algae as active components of communities. Perhaps, as suggested by Nienow (1996), this will not be resolved until molecular probes become available for use in the field.

5.4.5. Comparison of algae collected in Frisbees with those deposited onto snow

Direct counts of both Frisbee and snow samples were dominated by the cyanobacteria cf. *Gloeocapsa* and *Fischerella* sp. (Fig. 5.3.1, 5.3.3). However, there were fewer types of algae observed in snow samples (compare horizontal axes of Fig. 5.3.1 and 5.3.3). Three of the snow samples used for dispersal studies were grouped apart by the ordination (Fig. 5.3.7). This is due to the relatively rare occurrence of *C. aeruginosa* (present in 2 of 6 snow samples against 7 of 8 Frisbee samples) and presence of diatom species which have not been recorded from Mt Philistine habitat samples. These characteristics distinguish snow dispersal samples from both Frisbee and habitat samples on that day.

The most obvious contrast between Frisbee and snow samples is the virtual absence of algae found in plate counts from snow (Table 5.3.1). This raises questions about viability of algae blown onto snow, and is discussed in section 5.4.6.

5.4.6. Viability of algae in aerobiota

Very few algae grew on agar plates inoculated with snow samples and incubated at 14°C (Table 5.3.1). Algae detected by direct microscopic examination were present in these samples (Fig. 5.3.1) Culturable algae either do not survive in surface snow conditions (low temperature and desiccation) or they are lost from surface snow.

Algae from habitat samples on Mt Philistine survive freezing, as all samples were subjected to this before inoculation of cultures (section 5.2.2; Chapter 3). It is also possible to grow *Stichococcus* cf. *bacillaris* and *Pseudococcomyxa simplex* at 3°C (snow algae culture conditions) even though they were initially isolated at 14°C. Study of the tarn snow algae population has suggested that cells could be lost from the surface snow at an average rate of approximately 16-33 cells ml^{-1} surface snow day^{-1} (see

Chapter 4). Loss could also explain the lower species richness in surface snow compared to Frisbee samples. Therefore the evidence suggests that unicellular aerobiota are lost from surface snow.

At least some of the algae recorded in direct counts are also known to be viable when collected in Frisbees. Cf. *Gloeocapsa* was always recorded in direct counts (Fig. 5.3.3), but cells known to be viable were found only in lower basin samples on the first three sampling occasions (Fig. 5.3.5). Therefore, not all cells dispersed were viable on the culture medium used. *Phormidium* cf. *retzii*, found at low numbers in the low basin and once in the upper basin (Fig. 5.3.5) was never found in cultures from the same samples. However, it is possible that absence in culture has a reasonable probability when there are such low numbers in samples. *Klebsormidium* cf. *flaccidum*, found rarely and at low numbers in direct counts, had a similar distribution in cultures (Fig. 5.3.5).

Although no diatoms were cultured, I believe that this is due to inappropriate culture medium, rather than to non-viability of all the cells as suggested by Rosas *et al.* (1989). Some diatoms appeared to have living contents in direct microscopic observations. Likewise, the lack of growth of many other algae in culture (*Fischerella* sp., cf. *Ammatoidea*, desmids, etc) is not necessarily an indication of non-viability.

Viability of wind-dispersed snow algae cysts is unknown, due to difficulties in germinating them in culture (Hoham 1980, Hoham *et al.* 1983). *Raphidonema nivale*, which is known only to have a vegetative state (Hoham 1973), was not recorded in Frisbees. However it was rarely found in snow samples during the study period, so the probability of capturing any wind-dispersed cells would have been extremely low.

5.4.7. Effect of weather conditions on abundance of aerobiota

Plate counts of algae from Frisbees were significantly lower on 9 December than on prior days. Very strong winds occurred on 28-30 October and from 14-18 November 1999 (Fig. 5.4.1; also see Chapter 4). This could explain lower numbers of cultured cells in the 9 December sample, which was taken after a milder period of weather than the 26 November sample. This implies that more algae were dispersed at higher wind speeds, as expected (Broady 1996).

It is likely that dry conditions are not required for dispersal of some Mt Philistine algae. There is little bare soil at the study site and many algae are associated with the common *Andreaea* moss. This moss fragments more easily when it is dry.

However, strongest winds on the mountain occur during rain. During these conditions, moist fragments of moss and lichen could still be dispersed, at least by saltation.

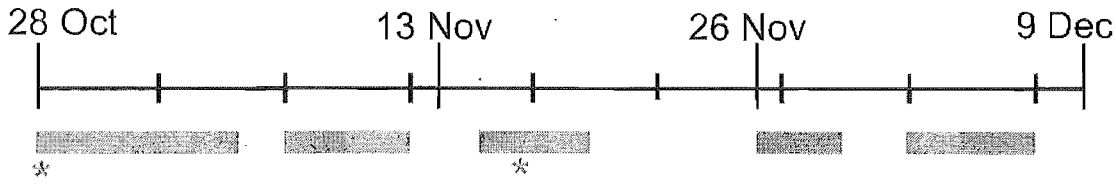


Fig. 5.4.1. Representation of weather conditions taken from qualitative data in Chapter 4 for the Frisbee sampling intervals for which standardised data is available. Dates are those on which Frisbee samples were taken. Shaded bars indicate major periods of rain, the first of which is approximate. No quantitative windspeed data are available, but days on which winds were particularly strong are indicated by asterisks. The time line is divided into 5-day increments.

5.4.8. Summary

Frisbee collectors were found to be appropriate for sampling the aerobiota on Mt Philistine, and standardisation of counts as proportions of the pollen count in each Frisbee provided an effective means to make comparisons between different locations and times.

Snow algae cysts are a very small proportion of the aerobiota on Mt Philistine. Although there is evidence that some process other than germination of cysts from the previous year initiates the snow algae bloom, the role of airborne dispersal of *Chlainomonas kolii* is still unknown. It appears that unicellular aerobiota is lost from surface snow in the same way as snow algal cells are lost during blooms in tarn surface snow.

Temporal variation in dispersal of certain culturable algae on the site is different from some other species. This may be related to the "r"-selected growth strategy of the former organisms and involve utilisation of nutrient-rich snowmelt during the spring. Milder weather during the later sampling interval may also have contributed to this observation.

CHAPTER 6.

TAXONOMY OF ALPINE ALGAE

6.1. Introduction

6.1.1. Prior studies of snow and terrestrial algae in New Zealand

The observation of New Zealand coloured snow was first recorded by the mountain guide Peter Graham in the 1890s (Hewitt 1965). Most coloured snow shown to be due to algae in New Zealand is red (Thomas and Broady 1997). Given the common nature of snow coloured by dust in summer it cannot be determined whether reports of other snow colours in this country are in fact due to algal blooms.

The first clear identification of a snow alga (*Sphaerellopsis rubra*) in a New Zealand sample was reported by Hardy (1966). This was followed by a tentative identification of *Chlamydomonas antarcticus* Wille in Gain from New Zealand by Kol (1968a). Wilson (1976) reported *Chlamydomonas antarcticus*, *C. nivalis*, *C. sanguinea* Lagerheim, and *Cryocystis brevispina* (=*Chloromonas brevispina* (Fritsch) Hoham, Roemer and Mullet) in Mount Cook National Park. Thomas and Broady (1997) identified *Chlamydomonas*, *Cryocystis*, *Scotiella*, *Trochiscia*, *Koliella*, and *Raphidonema* from New Zealand samples.

No New Zealand snow algae have been cultured. Given the importance of cultures (Hoham 1973) and the questionable nature of some of the genera reported (Hoham and Mullet 1977), such as *Scotiella* and *Cryocystis*, culturing is clearly a priority to increase reliability of taxonomy of New Zealand snow algae.

The most detailed floristic study of New Zealand alpine algae prior to the present was made in Mt Cook National Park (Wilson 1976). Habitats from montane to alpine and nival altitudes were sampled, including tarns and pools, soil, wood, rock, streams and snow. Most of the 63 algae were identified to genus level, and no cultures were used. There were 38 distinct chlorophyte, 11 cyanophyte, 4 chrysophycean, 3 dinoflagellate and 7 diatom taxa. Xanthophyceans were not observed.

In general, the terrestrial algal flora of New Zealand is poorly known. Flint (1958) investigated the algal flora of some tussock grassland soils; however, no algae were identified beyond class level. A more detailed study followed of the surface of 28 New Zealand soils carrying forest, scrub and pasture (Flint 1968). Algae identified were the cyanophytes *Scytonema hofmanni* Agardh, *Nostoc muscorum* Agardh, and *N. commune* Vaucher; the chlorophytes *Gongrosira* sp., *Chlorhormidium flaccidum*, *Cosmarium* sp., *Euastrum* sp., and *Zygogonium* sp.; the xanthophyceans *Heterothrix*

exilis (Klebs) Pascher, *Heterococcus* sp., *Tribonema* sp., and *Vaucheria* sp.; *Euglena* sp.; and the diatoms *Hantzschia amphioxys* (Ehrenberg) Grunow, and *Pinnularia borealis* Ehrenberg. The algal flora of the Snares Islands was also described (Fineran 1969, Flint and Fineran 1969). Although distributions of the algae were not always given, at least 18 taxa were present in terrestrial habitats. The chlorophytes *Chlamydomonas* sp., *Chlorella* sp., *Chlorhormidium flaccidum*, *Coccomyxa* sp., and *Stichococcus bacillaris*, the cyanophytes *Microcoleus vaginatus* (Vaucher) Gomont and *Nostoc* sp., the diatom *Achnanthes* sp., and the euglenoid *Euglena* sp., were all present on peats under vascular plants.

Two studies with agricultural objectives enumerated algae in grassland soils. Among non-symbiotic nitrogen-fixing micro-oganisms in soils from the MacKenzie Basin, Central Otago and inland Canterbury were the cyanophytes *Anabaena* sp., *Nostoc* sp., and *Tolypothrix* sp. (Line and Loutit 1973). More than 87% of algae grown on BBM agar from Taita and Judgeford soils were unicellular chlorophytes, *Chlorella* sp. and *Stichococcus* sp. being most common (Ramsay and Ball 1983).

However, the most detailed study on terrestrial New Zealand algae to date is that of Everett (1998). Thirty-nine taxa were identified from soils in the Cass Basin using moist soil enrichment and agarised mineral salts cultures, and descriptions and illustrations of most algae were provided. Eight cyanophytes, 24 chlorophytes, 2 xanthophyceans, 3 diatoms, 1 eustigmatophycean and 1 dinoflagellate were recorded.

To gain an improved knowledge of the algal flora of New Zealand alpine environments, there is a clear need to examine samples from a wide range of habitats using a synthesis of direct microscopic examination and culture techniques. This approach allows identification of small unicellular algae, elucidation of life cycles of those such as the snow algae, which are often present as resting stages in field samples, and differentiation between algae which appear very similar in direct microscopic examination. Particularly small algae may be overlooked completely without cultures. The observational detail necessary to separate many chlorophytes can be achieved only using cultures. For conclusions regarding their biogeography to have any meaning, their identification must be reliable.

6.1.2. Problems and approaches in the taxonomy of snow algae

Taxonomic problems amongst alpine algae in general do not differ greatly from those found elsewhere, and they are well described in recent texts (e.g. Van den Hoek *et al.* 1995, Graham and Wilcox 2000). However, the complex ecology of snow algae creates certain problems. An overview of approaches to their taxonomy is therefore important in order to understand the considerable taxonomic confusion which has surrounded identification of many of these organisms in the past.

Chlamydomonas nivalis was the first snow alga to be described, and is the most commonly reported species in the northern hemisphere (Garric 1965). *C. nivalis* was the only species common to all sites investigated in seven states of the U.S.A. (Wharton and Vinyard 1983). However, more than fifteen morphological cell types have been recorded for this species, prompting the suggestion that it is a collective species covering several different species of *Chlamydomonas* (Kol 1968b). If this is so, then the different species could have different biogeographical distribution patterns.

A major problem in taxonomy of snow algae has been the misidentification of resting stages as independent species. Fritsch (1912) commented that it "can hardly be doubted that some species of *Trochiscia* are merely resting stages of other algae". Fukushima (1963) believed that cells named as *Chodatella brevispina* in Japan may have been a stage in another alga's life history. The study of life cycles for confident identification was taken an important step further when Stein and Amundsen (1967) followed the development of organisms through observations shortly after collection. However, the comprehensive text by Kol (1968b), which listed over 300 species, described many erroneously classified resting cysts.

Many of the classifications used in publications prior to 1980 have now been revised considerably. Culture work has shown that zygotes of *Chloromonas pichinchae* (Hoham 1975), *C. nivalis* (Hoham and Mullet 1977), *C. brevispina* (Hoham *et al.* 1979), and *C. polyptera* (Hoham *et al.* 1983) corresponded to species previously placed in the genera *Scotiella*, *Trochiscia*, and *Cryocystis*.

Fott (1976) erected the genus *Scotiellopsis*, which has the habit of *Scotiella* but reproduces by autospores. This genus is usually found in soils and other non-snow habitats (Punčochářová and Kalina 1981). Molecular techniques have now shown that the family Scotiellocystoideae should be removed from the Chlorellaceae where it was

originally placed (Hanagata 1998). Interestingly, Hanagata (1998) advocated retaining the genus *Scotiella* for those species in which reproduction is unknown.

When cultures of snow algae are not successful, description of field material can be difficult. This can lead to controversy. For example, Hardy and Curl (1968) described a new species of *Trachelomonas* causing red snow. Hoham (1974a), examining the same material, described observations contrasting with those of the previous authors, including different chloroplast shapes and numbers, the presence of starch, and a different outer envelope structure. Erection of the species *Chlainomonas kolii* was the result.

Some studies have reported growth of species in cultures of snow meltwater which were not observed in the original sample, for example *Chromulina chionophila* (Stein 1963) and *Cryptomonas frigoris* (Javornicky and Hindák 1970). The obviously low numbers of these algae in the original samples suggest they may have been present as wind-blown propagules (*Stichococcus bacillaris* is a common example of this). However, the obligate growth temperatures of these organisms (<10°C) show that they are true snow algae. *Chromulina chionophila* has been reported since in the field (e.g. Hoham *et al.* 1989).

Studies of snow algae communities have seldom examined species growing in surrounding habitats (exceptions include Wilson 1976, Mataloni and Tesolin 1997, Ling and Seppelt 2000). The possibility that some species growing in the snow are present, and perhaps capable of growth, in other environments is discussed in Chapter 3 (Distribution Patterns).

Examination of cultured material must be reinforced with observations of field specimens, as cells which are cultured may change in appearance. For example, a change of temperature in culture may change a *Chodatia* cell into a *Stichococcus* type, and *Chlamydomonas* cells may have a more developed papilla when cultured (Fukushima 1963). The power of combining culture work with field observations was shown by Hoham (1971, 1973), who obtained a pure culture of the green snow alga *Raphidonema nivale* on PFW medium. In ageing cultures the filaments of *R. nivale* dissociated into unicells which strongly resembled *Koliella* and *Stichococcus* species in field samples, and changed morphology in response to different nutrient levels. These findings demonstrated the need to culture species in the *Raphidonema-Koliella* complex before making taxonomic decisions (Hoham 1973).

6.1.3. Aims

Which algae grow in the alpine zone on Mt Philistine? To answer this question, the following has been attempted.

- To thoroughly describe the flora of all terrestrial and snow habitats.
- To combine culture work with field observations, in order to elucidate life-cycles of snow algae.
- To compare the described flora with other alpine areas, Antarctica, and New Zealand sites for which the algal flora is known.

6.2. Methods

Samples were collected in February 1998, April 1999 and December 1999 from the Mt Philistine study site. Collection, examination and culture procedures are described in Chapter 3: Distribution.

Algae were classified according to the following taxonomic systems.

- Cyanobacteria: Komárek and Anagnostidis (1998, Chroococcales); Anagnostidis and Komárek (1988, Oscillatoriales); Komárek and Anagnostidis (1989, Nostocales); Anagnostidis and Komárek (1990, Stigonematales).
- Euglenophyta, Chlorophyta: Ettl and Gärtner (1995).
- Heterokontophyta: Starmach (1985, Chrysophyceae); Krammer and Lange-Bertalot (1991a, b, 1997a, b, Bacillariophyceae); Ettl (1978, Xanthophyceae).

Arrangement of descriptions of each taxon. Identifications were taken to the lowest taxonomic level possible with the information obtained. Where uncertainty exists it is indicated by "cf." Illustrations of Mt Philistine specimens of each taxon are indicated after its name. Citations of literature used in identification are provided on the following line. Habitats in which each alga was found are then given (for more detailed information on distribution patterns, refer to Chapter 3: Distribution). The key to these codes is shown in Table 6.1.

The code in brackets following the distribution information refers to the examination method(s) in which the alga was recognised. The key to this code is as follows.

DE = direct microscopic examination of sample.

EC = moist plate enrichment culture.

MC = mineral salts culture (liquid for snow algae, agarised for others; almost always unialgal isolates).

Table 6.1. Key to codes used to describe distribution of taxa in this chapter.

Type of habitat	Code	Description of sample material
Edaphic	SO	Organic soil, lacking visible vegetation.
	MF	Mineral fines, lacking visible vegetation.
Epilithic	R	Rock surfaces, including samples of lichens.
Epiphytic	LM	Leaves and stems of mosses.
	LV	Leaves and stems of vascular plants.
Aquatic	P	Benthic and suspended material from pools in rock surfaces.
Snow	SN	Snow surface samples.
Aerobiota	ASN	Airborne material deposited onto snow.[1]
	A	Airborne material deposited into samplers.[1]

[1] See Chapter 5 (Dispersal) for sampling procedures.

Detailed description of the organism follows. Vegetative and reproductive features are described, followed by remarks about reliability of the identification, comparisons with other literature, and whether the alga is likely to be a new record for New Zealand. The latter comments are based on the species lists of Cassie (1984) and diverse literature derived from these. Except for the snow algae, no attempt has been made to obtain more recent information on New Zealand records, due to the scattered nature of the literature.

6.3. Descriptions of algae

Division Cyanophyta

Class Cyanophyceae

Order Chroococcales

Family Synechococcaceae

Subfamily Aphanothecoideae

***Cyanothece aeruginosa* (Nägeli) Komárek** Fig. 6.1a-d, i-n.

Komárek and Anagnostidis (1998) p49-50, Fig. 28. Bourrelly (1970) p568. Komárek and Cepak (1998) p25-39.

Distribution: R, P, MF, SO, LM, LV, ASN (DE, EC)

Vegetative features. Cells single or in pairs following division, broadly ellipsoidal to cylindrical with rounded ends, 28-41 μm long, 17-22 μm wide (length:width = 1.3 - 2.0), surrounded by thin mucilage envelope. Protoplasm granular, sometimes striated lengthwise, with large vacuoles in older cells (Fig. 6.1a,d).

Reproductive features. Simple division in one plane forms two identical daughter cells (Fig. 6.1b,c). Transverse wall at cell equator perpendicular to longer cell axis (Fig. 6.1k). Daughter cells remain attached at mucilage layer before separation (Fig. 6.1l,m). Newly divided cells initially have one apex more broadly rounded than other (Fig. 6.1n), and enlarge to adult size before further division.

Remarks. Division in only one plane, which distinguishes this alga from the morphologically similar *Synechococcus* and *Synechocystis* (Bourrelly 1970) can be inferred by formation of transverse wall perpendicular to longitudinal axis, and growth of daughter cells to adult size before release. The cell size and shape, keritomised chromoplasm, and fine mucilage layer around cells are characteristic of *C. aeruginosa* (Komárek and Anagostidis 1998).

C. aeruginosa is reported from moorland/peaty waters, raised bogs and wet rocks, from lowlands to mountains and temperate to polar ecosystems (Komárek and Anagostidis 1998). It has been reported from New Zealand (as *Synechococcus aeruginosus* and *Coccochloris aeruginosa*) in Taupo soil (Cassie 1984), in rain pools on rock surfaces in Mt Cook National Park (Wilson 1976), and Omarama soil on Hen Island (Loach 1954).

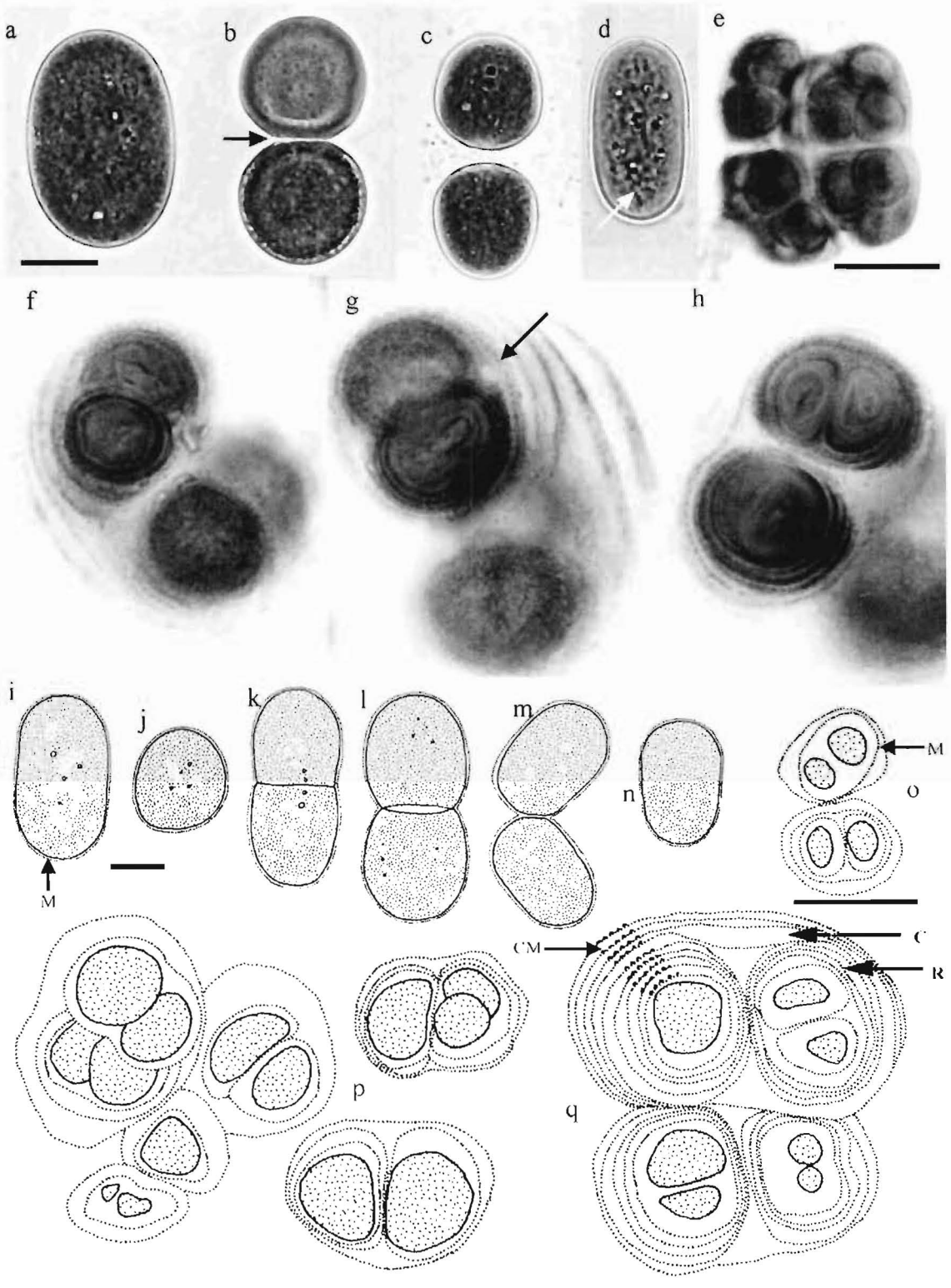


Fig. 6.1. a-d. i-n. *Cyanothece aeruginosa*. field material: a. mature cell; b-c. cell division (arrow indicates cells joined by mucilage); d. mature cell showing keritomy within chromoplasm (arrow); i. mature cell. M=thin mucilage surrounding cell; j. transverse optical section of cell; k-m. cell division; n. new daughter cell.

e-h. o-q. cf. *Gloeocapsa*. field material: e. developing colony; f-h. mature colonies. note wart-like processes on mucilage (arrow); o. young cells with blue-green chromoplasm resembling *Chroococcus* (M=concentric colourless mucilage layers); p. maturing cell groups with red chromoplasm; q. mature cells (CM=example of crenellations which occurred over all mature mucilage lamellae. R=red mucilage layers. C=colourless mucilage layers).

All scales=10 µm (use scale in a for a-d; e for e-h; j for i-n; o for o-q).

Subfamily Microcystoideae

cf. *Gloeocapsa* Kützing Fig. 6.1e-h, o-q.

Komárek and Anagnostidis (1998) p236, 253, Fig. 329.

Distribution. P, SO, MF, LM, LV, ASN (DE)

Vegetative features. Colonies microscopic to macroscopic, consisting of clustered mucilaginous aggregates of cells. Cells spherical to rounded polygonal, 4-9 μm long by 3-8 μm wide, with blue-green contents. Mucilage lamellate; young cells surrounded by up to 3 concentric, smooth, colourless layers (Fig. 6.1o); old cells surrounded by up to 10, with densely distributed conical processes on surface (Fig. 6.1n-q), inner layers red, becoming colourless towards periphery.

Reproductive features. Division in three planes. Older colonies with conical processes on mucilage (Fig. 6.1q, i.e. "*Asterocapsa*" form) may be a resting stage.

Remarks. Mucilage with a smooth margin in younger stages suggests that this alga is *Gloeocapsa*. Other features such as mucilage pigmentation and cell arrangement are shared with species of *Asterocapsa* in the Chroococcaceae. The cells are commonly not spherical, whereas Komárek and Anagnostidis (1998) state that cells of *Gloeocapsa* are "almost always" spherical. Cell division in the Microcystaceae gives rise to spherical cells, whereas non-spherical cells are produced in the Chroococcaceae. However, conical processes on the mucilage surface of *Asterocapsa* are present throughout the life history (Komárek and Anagnostidis 1998), whereas they only appear on mature stages of the Mt Philistine specimens (Fig. 6.1n-q).

Gloeocapsa and *Asterocapsa* species are often epilithic, sometimes in high mountain regions, in fresh water habitats including thermal springs (Komárek and Anagnostidis 1998).

Family Chroococcaceae

***Chroococcus* sp. Nägeli** Fig. 6.2a, e-h.

Komárek and Anagnostidis (1998) p 279-281, 284, Fig. 376.

Distribution. P, MF, LM, LV (DE, EC)

Vegetative features. Young cells in packets of 2-8, old cells in irregular arrangements (Fig. 6.2a); cells blue-green, spherical to hemispherical, 5.0-7.0 μm long, 4.5-7.0 μm wide, surrounded by colourless, non-lamellate mucilage (Fig. 6.2e-g).

Reproductive features. Cell division in 3 perpendicular planes (Fig. 6.2h).

Remarks. *Chroococcus* is reported from freshwater ponds, lakes and moorland waters, as free-living, epiphytic cells or as periphyton, rarely aerophytic (Komárek and Anagnostidis 1998).

Family Xenococcaceae

cf. *Myxosarcina* Printz Fig. 6.2b-d, i-k.

Komárek and Anagnostidis (1998) p426, Fig. 556, 557, Table 4.

Distribution. MF, R, SO, P, ML (EC, MC)

Vegetative features. Colonies consisting of irregular closely-packed mucilaginous aggregates of rounded-polygonal cells (Fig. 6.2b, j). Cells 3-6 μm long by 2-4 μm wide, spherical to irregularly rounded when solitary (Fig. 6.2i), surrounded by very thin mucilage. Contents blue-green, chromoplasm usually peripheral (Fig. 6.2b, c).

Reproductive features. Division (Fig. 6.2c, k) in three planes. Baeocytes formed within mucilaginous cell packets (Fig. 6.2k).

Remarks. Mode of division and baeocyte production place the alga in Xenococcaceae. Cell shape, lack of polarity, colony morphology, and thin and delimited mucilage support assignment to *Myxosarcina*. However, species described by Komárek and Anagnostidis (1998) are reported to have homogeneous chromoplasm. Cells also closely resemble *Chroococcidiopsis*, but may be distinguished from this genus by rounded-polygonal shape of cells when in packet-like colonies (Komárek and Anagnostidis 1998, p420).

At least one species of *Myxosarcina* (*M. tatrica* (Starmach) Komárek & Anagnostidis) is found on moistened rocks in high mountain regions (Komárek and Anagnostidis 1998). The genus does not appear in species lists from New Zealand (Cassie 1984).

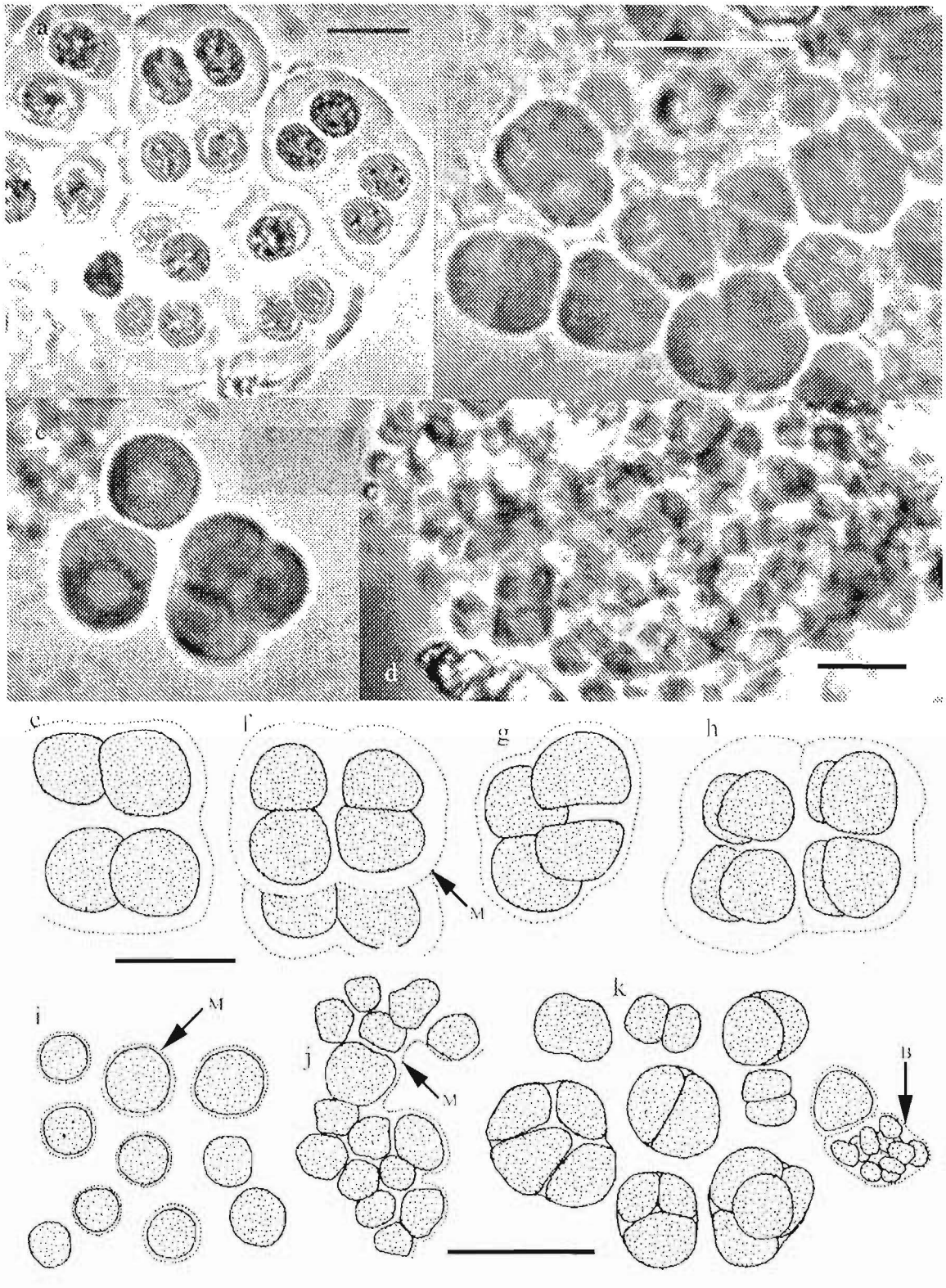


Fig. 6.2. a, e-h, *Chroococcus* sp., moist plate enrichment material: a, mature colony; e-h, typical cell tetrads (M= colourless mucilage).

b-d, i-k, cf. *Myxosarcina*, agarised culture material: b, c, cell packets; d, mucilage shown in Indian ink preparation; i, solitary unicells (M=thin mucilage surrounding cells); j, portion of mucilaginous colony (M=mucilage); k, dividing cells giving rise to cell packets (B= baeocyte).

All scales=10 μm (use scale in b for b-c; e for e-h; k for i-k).

Order Oscillatoriales

Family Phormidiaceae

Subfamily Phormidioideae

***Phormidium* cf. *retzii* (Agardh) Gomont** Fig. 6.3a-c, f-h.

Geitler (1932) p 1012-1013, Fig. 647a-d. Anagnostidis and Komárek (1988) p402, Fig. 1, Table 2.

Distribution. P, SO, MF, LM, LV (DE, EC, MC)

Vegetative features. Trichomes with individual, thin, colourless non-lamellate mucilage sheaths; gliding motility; straight and flexuous (Fig. 6.3a, b, f); 4-6 μm wide; apical 3-4 cells straight and attenuated (Fig. 6.3a, f, g). Cells shorter than wide to nearly isodiametric (length:width = 0.13 - 0.77), 1-4 μm long, commonly granulated, with very slight constrictions at cross walls. Apical cell rounded to conical, frequently with calyptra (Fig. 6.3a, b, f, h).

Reproductive features. Necridic cells and hormogonia (Fig. 6.3h).

Remarks. Freshwater habitat, trichome width, cells touching rather than separated, and tapered terminal region suggest *P. retzii* (Geitler 1932). However, the size range is at the low end of that reported and some of the terminal cell shapes illustrated by Geitler (1932) have not been observed.

P. retzii has been reported as cosmopolitan in flowing and stagnant water. It is not recorded in species lists from New Zealand by Cassie (1984).

cf. *Phormidium* sp. 2 Fig. 6.3d, n, o.

Anagnostidis and Komárek (1988) p409, Fig. 4, Fig. 10, Table 5, Table 6.

Distribution. ML (DE)

Vegetative features. Trichomes 5-8 μm wide, with individual colourless mucilage sheaths up to 2 μm thick (Fig. 6.3d, n), may be lamellate, especially where hormogonia are present (Fig. 6.3o). Cells approximately isodiametric to longer than wide (length:width = 1.0-1.6), 5-8 μm long, 4-6 μm wide, with pronounced constrictions at cross walls (Fig. 6.3n). Apical cell slightly attenuated with rounded end.

Reproductive features. Hormogonia. No necridic cells noted.

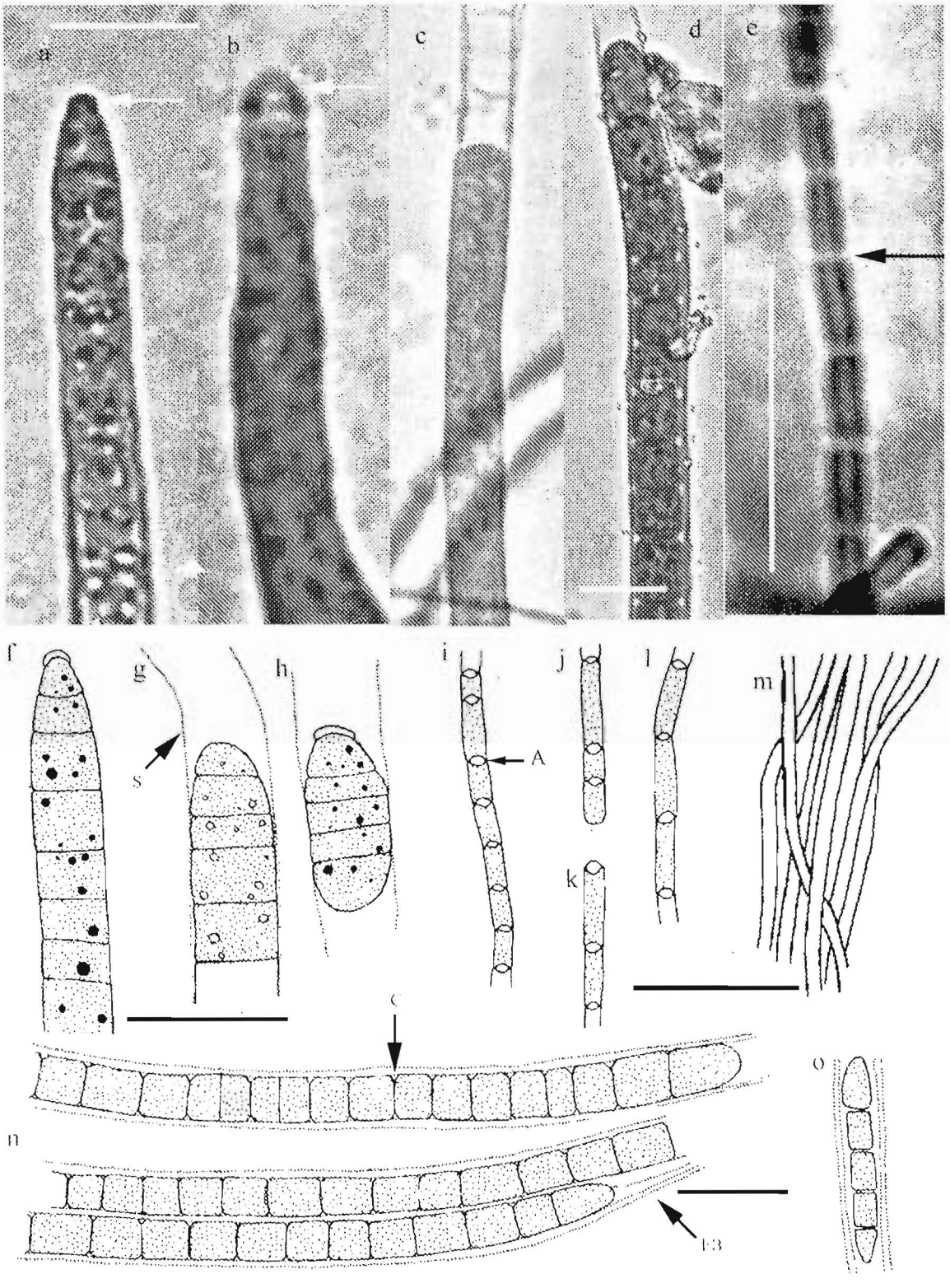


Fig. 6.3. a-e, f-h, *Phormidium* cf. *retzii*. culture material: a, b, mature trichomes with calyptra (arrows); c, healthy trichome; f, terminal region of trichome with calyptra; g, terminal region of fragmented trichome within sheath (S), lacking calyptra; h, hormogonium.

d, n-o, cf. *Phormidium* sp. 2, field material: d, trichome terminal region; n, trichomes, with prominent constrictions at transverse walls (C); o, hormogonium with narrower cells.

e, i-m, *Pseudanabaena* cf. *tenuis*, agarised culture material: e, i, trichomes with aerotopes (A, arrow); j, terminal region of trichome with no aerotope visible in terminal cell; k, terminus with aerotope; l, m, growth form in culture.

All scales = 10 µm (use scale in a for a-e; g for f-h; m for i-m; n for n-o).

Remarks. Necridic cells, a feature of the Phormidiaceae, were not observed, probably due to insufficient examinable material. Each sheath contains only one trichome (Fig. 6.3n shows adjacent trichomes in separate sheaths), placing it in the Phormidioideae. Assignment to *Phormidium* is based on cell and trichome shape and absence of false branching (Anagnostidis and Komárek 1988); however more material is required for confident identification.

Subfamily Microcoleoideae

cf. *Microcoleus* Desm. ex Gomont Fig. 6.4e-g.

Anagnostidis and Komárek (1988) p419, 440, Table 2, 5, 13.

Distribution. SO (DE)

Vegetative features. Trichomes straight (Fig. 6.4e) to slightly curved (Fig. 6.4f), 4-6 μm wide; gliding motility; sheath colourless, 1-5 μm thick, containing 1-3 trichomes (Fig. 6.4g); cells 4-11 μm long, no constrictions at transverse walls, apical cells rounded.

Reproductive features. None observed.

Remarks. Multiple trichomes per sheath is characteristic of Schizotrichaceae or Phormidiaceae (subfamily Microcoleoideae). Motility of trichomes and lack of a tapered conical sheath excludes the alga from the Schizotrichaceae. Within Microcoleoideae, Anagnostidis and Komárek (1988, p419) viewed the definition of genera to be unsatisfactory and sheath morphology to be the sole diacritical feature. Sheath morphology places this alga in the genus *Microcoleus*, since the nearest alternative, *Hydrocoleum*, has a lamellated mucilage sheath (Anagnostidis and Komárek 1988).

The alga can be placed with confidence in the family Phormidiaceae, based on trichome characteristics and irrespective of sheath morphology. More specimens are required to identify the alga confidently beyond this level.

Family Pseudanabaenaceae

Subfamily Pseudanabaenoideae

***Pseudanabaena* cf. *tenuis* Koppe** Fig. 6.3e, i-m.

Geitler (1932) p932, Fig. 596b. Anagnostidis and Komárek (1988) Fig. 18, 21; Table 3. Bourrelly (1970) p438-439.

Distribution. LM, MF, SO, P, R (DE, EC, MC)

Vegetative features. Trichomes flexuose; constricted at transverse walls; 1-2 μm wide (Fig. 6.4.e, i-l). Sheath absent. Waving motility. Cells longer than wide (length:width = 1.3-5.0), 1.5-8.0 μm long. Gas vacuoles (aerotopes) occur as bright regions at cell apices (Fig. 6.4e), but vesicles within cannot be resolved in LM. Chromoplasm peripheral (Fig. 6.4e).

Reproductive features. Filaments readily fragment.

Remarks. The alga belongs in *Pseudanabaena* rather than the morphologically similar *Romeria* because it exhibits waving motility (Anagnostidis and Komárek 1988). Cell dimensions are characteristic of *P. tenuis*, although cell shape is closer to the larger *P. catenata* Lauterb. TEM would give more information about structure of aerotopes.

The species has been reported from mud, humus and littoral zones (Geitler 1932). The genus *Pseudanabaena* is not reported in species lists from New Zealand (Cassie 1984).

Subfamily Leptolyngbyoideae

***Leptolyngbya* Anagnostidis & Komárek sp. 1** Fig. 6.4a, b, h-k.

Anagnostidis and Komárek (1988) p380, 439, Table 3.

Distribution. MF, P, LM (MC)

Vegetative features. Trichomes immotile with very thin, colourless mucilage sheath (Fig. 6.4j); flexuose with straight apices; slightly constricted at transverse walls (Fig. 6.4a, b, i); 1.5-3 μm wide. Cells isodiametric or wider than long (width:length = 0.8-4.0), 0.5-2.5 μm long. Apical cells straight, rounded to conical (Fig. 6.4i); calyptra absent.

Reproductive features. Necridic cells absent.

Remarks. Absence of necridic cells places the alga in Pseudanabaenaceae. Sheath and immotility assign it to Leptolyngbyoideae, and distinguishes the organism from

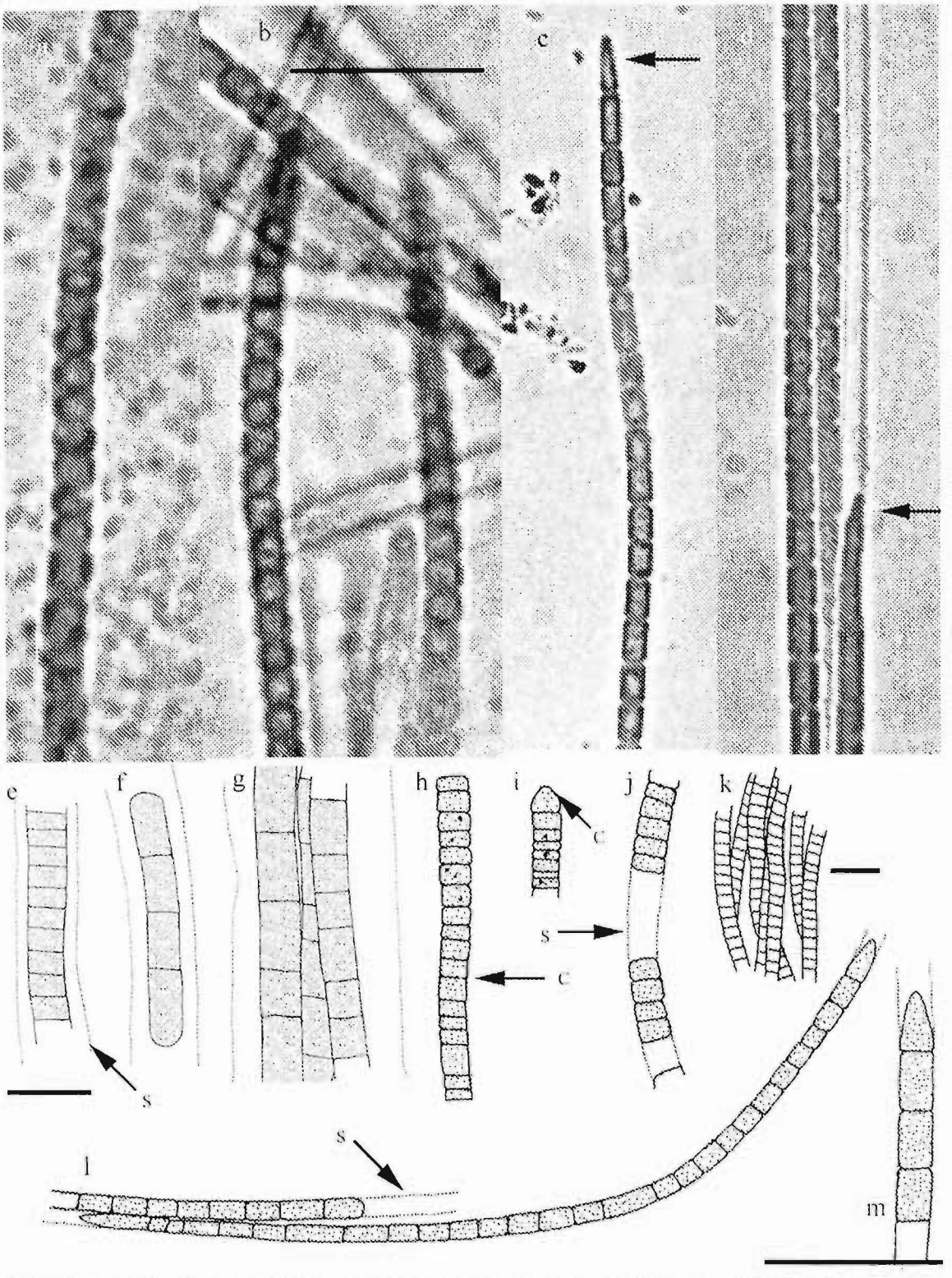


Fig. 6.4. a, b, h-k. *Leptolyngbya* sp. 1, agarised culture material: a, b, typical trichomes; h, portion of trichome, note constrictions between transverse walls (C); i, trichome terminus showing conical terminal cell (C); j, trichome with missing cells showing thin sheath (S); k, group of trichomes showing growth pattern in culture.

c, d, l, m, cf. *Leptolyngbya* sp. 2, agarised culture material: c, d, trichome, note strongly attenuated terminal cells (arrows); k, trichomes with thin sheath visible (S); l, detail of trichome terminal region.

e-g, cf *Microcoleus*, field material: e, f, single trichomes within sheaths (S), showing variable cell length; g, three trichomes in single sheath.

All scales=10 µm (use scale in b for b-d; e for e-j, l).

Pseudanabaena Lauterb. It can exist as a free cluster of tangled trichomes (Fig. 6.4k), characteristic of *Leptolyngbya* (Anagnostidis and Komárek 1988).

Species lists from New Zealand (Cassie 1984) pre-date the erection of this genus. It is possible that both species of *Leptolyngbya* have been included as species of *Lyngbya*, *Phormidium* or *Plectonema*.

cf. *Leptolyngbya* Anagnostidis & Komárek sp.2 Fig. 6.4c, d, l, m.

Anagnostidis and Komárek (1988) p366-367, 389-390, Table 2.

Distribution. MF, P, LM (EC)

Vegetative features. Trichomes 2.0-3.0 μm wide, constricted at transverse walls (Fig. 6.4c, d), motile by gliding within very thin, colourless sheath. Cells longer than wide (length:width = 1.3-1.7), 3-5 (-8) μm long. Terminal cells strongly attenuated at apex (Fig. 6.4c, d, m). Aerotopes absent. Chromoplasm peripheral.

Reproductive features. Filaments readily fragment.

Remarks. Trichome shape, peripheral chromoplasm and absence of necridic cells during trichome division suggest placement in Pseudanabaenaceae. However, gliding motility within the sheath is reported to be absent in this family (Anagnositidis and Komárek 1988, p376). Constrictions at cross walls and peripheral chromoplasm, and absence of aerotopes and granulation inside the cells, tentatively place the alga in the genus *Leptolyngbya*. Variants within *Pseudanabaena* may also share these features, but only subgenus *Ilyonema* has trichomes up to 3 μm wide, and this subgenus always contains aerotopes. Anagnostidis and Komárek (1988) groupéd cells with characteristics (except motility) of the Mt Philistine strain into "LPP group B" (Rippka *et al.* 1979) which they also termed the genus *Leptolyngbya*.

Leptolyngbya sp.2 can be distinguished from sp.1 from Mt Philistine because the latter has much shorter cells and less attentuated terminal cells.

Family Homoeotrichaceae

Subfamily Ammatoideoideae

cf. *Ammatoidea* West & West Fig. 6.5.

Anagnostidis and Komárek (1988) p327-472. Broady and Ingerfeld (1999) Fig. 3, 4, 6, 7. Anagnostidis and Pantazidou (1991) Fig. 18, 19.

Distribution. P, MF, R, LM, LV, ASN (DE, EC, MC) .

Vegetative features. Trichomes tapered, with laminated golden-brown sheath. Trichome heteropolar, with broad rounded terminal cell at ensheathed end (Fig. 6.5h), or isopolar, with a tapering apex protruding from each end of sheath (Fig. 6.5g). False branching also occurs (Fig. 6.5f). Cells 4-7 μm wide by 5-10 μm long in central region of trichome, tapering to 3-4 μm wide by 3-13 μm long, barely pigmented and protruding from sheath, at apices (Fig. 6.5a, i, j). These non-pigmented tapering terminal cells are absent when grown on agarised 5% BG11 medium (Fig. 6.5d, e).

Reproductive features. Reproduction of trichome by hormogonia formed in apical region (Fig. 6.5e, f, seen in culture when apices clearly living) or by division in central region (Fig. 6.5g, seen in field material). No necridic cells observed. Cell division in meristematic zone at base of tapering tip of trichome (Fig. 6.5g).

Remarks: The tapering trichomes of this organism suggests the genus *Ammatoidea*. Possibly, heteropolar trichomes observed in the same samples as isopolar ones are *Homoeothrix* rather than *Ammatoidea*; however, an isopolar trichome was observed to begin to fragment in the middle golden-sheathed region (Fig. 6.5g), which could produce two heteropolar trichomes. Some heteropolar trichomes could be *Calothrix* lacking a basal heterocyst. However, *Calothrix* growing in moist plate enrichments, presumably containing no less nitrogen than habitat samples, still had a basal heterocyst. Broady and Ingerfeld (1999) and Anagnostidis and Pantazidou (1991) showed convincingly that the heteropolar tapering condition lacking heterocysts is stable, due to absence of heterocyst differentiation and very poor growth on medium lacking combined nitrogen. However, because the Mt Philistine specimen has not yet been cultured in this way, a heteropolar form with heterocysts present (i.e. *Scytonemopsis*) cannot be completely ruled out (although no such organism was seen in exhaustive examination of sample collections); nor can coiling morphology, occasional absence of attenuation, and twisting within the sheath be confirmed, as described by Broady and Ingerfeld (1999).

Ammatoidea species have been found in a range of environments, from freshwater and marine habitats and thermal springs to temperatures below freezing in

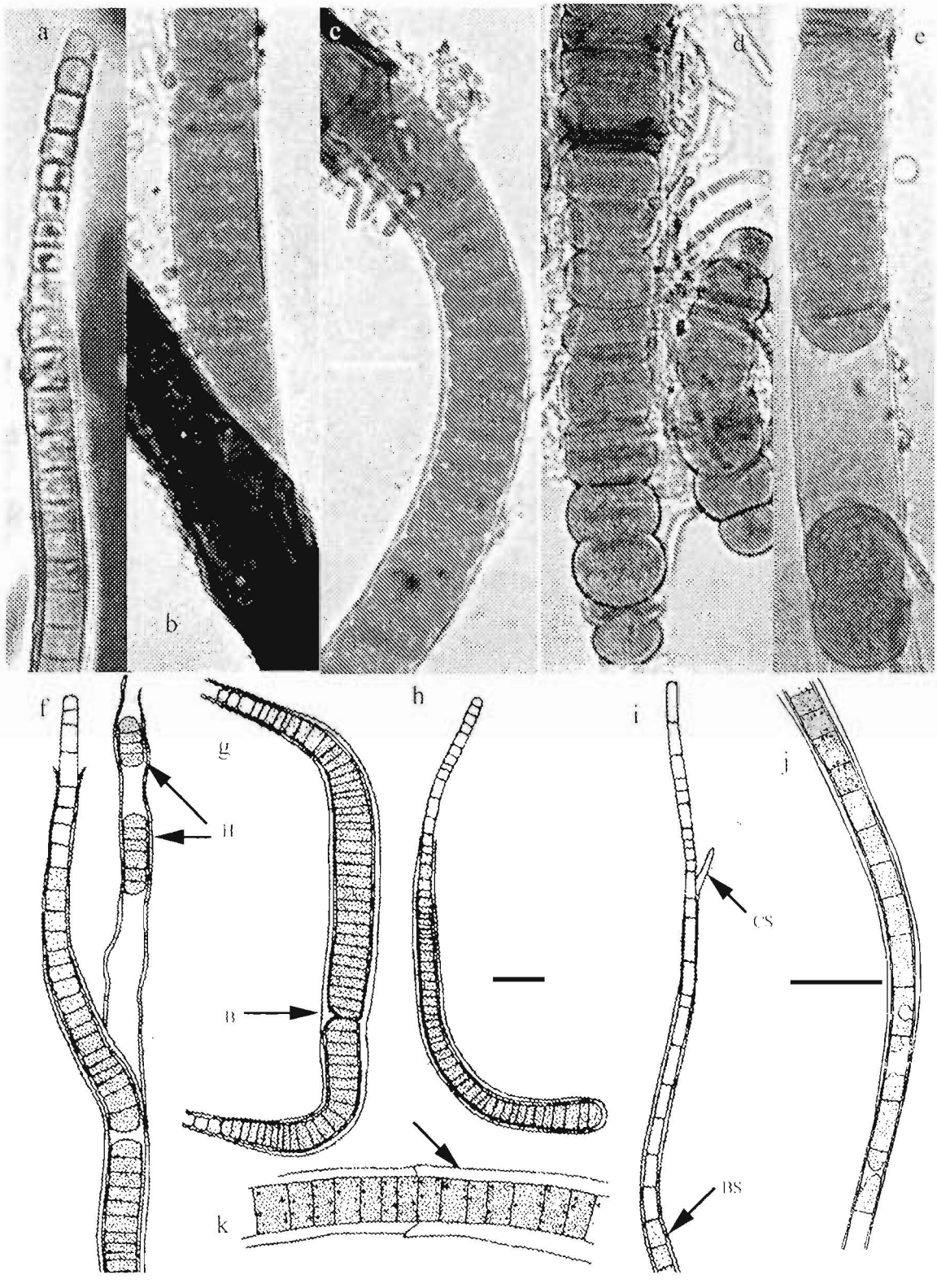


Fig. 6.5. a-j, cf. *Ammatoidea*, field material: a, attenuated trichome terminus with unpigmented cells; b, c, pigmented cells emerging from golden-brown sheath; f, trichome with hormogonia (H) in old sheath; g, complete isopolar trichome, note point of trichome breakage (B); h, heteropolar trichome; i, detail of tapered terminal region (CS=colourless sheath, BS= brown sheath); j, transition between pigmented and non-pigmented cells in terminal region; k, layering in golden-brown sheath (arrow indicates outer layer); agarised culture material: d, terminal region of growing trichome (note rounded cell shape); e, growing cells in sheath.

All scales=10 µm (use scale in e for a-e, use scale in h for f-i and k).

Antarctica (Anagnostidis and Pantazidou 1991, Broady and Ingerfeld 1999). *Ammatoidea normanii* West & West was reported from a brackish lagoon on the Chatham Islands, New Zealand (Cassie 1984).

Family Oscillatoriaceae

Subfamily Hormoscilloideae

***Hormoscilla* sp. Anagnostidis & Komárek** Fig. 6.6a, d-i.

Anagnostidis and Komárek (1988) p441, Table 2, 10, 13.

Distribution. P, MF, SO, LM, LV (DE, EC)

Vegetative features. Trichomes with very thin colourless mucilage sheath (Fig. 6.6d, e, g); non-motile; straight (Fig. 6.6d) to slightly curved (Fig. 6.6f); circular in transverse section; slightly constricted at transverse walls; no more than ~25 cells in length; 7-9 μm wide. Intercalary cells always shorter than wide (Fig. 6.6f, length:width = 0.13-0.43), 1-4 μm long; terminal cells 5-8 μm long with rounded ends.

Reproductive features. Necridic cells and non-motile hormogonia (Fig. 6.6g, h, i).

Remarks. Table 10 of Anagnostidis and Komárek (1988) states non-motility of trichomes is diacritical in the Hormoscilloideae, but *Katagnymene* (p425), a member of this subfamily, may be "indistinctly gliding". Thus lack of motility, lack of a gelatinous envelope and the cylindrical intercalary cells are the basis for assigning the Mt Philistine specimen to the genus *Hormoscilla*.

Order Nostocales

Family Nostocaceae

Subfamily Nostocoideae

***Nostoc paludosum* Kützing** Fig. 6.7a, d.

Geitler (1932) p836-7, Fig. 528a. Komárek and Anagnostidis (1989) p306, 316, Fig. 21, Table 7, Table 8. Bourrelly (1970) p424, 427, Fig. 124.

Distribution. MF, LV, P (EC, MC)

Vegetative features. Trichomes grouped in irregular colonies enclosed in colourless, lamellate mucilage (Fig. 6.7a). Trichomes curved, not tapered, isopolar; vegetative cells ellipsoidal to sub-spherical, 3.0-5.0 μm long, 3.5-6.0 μm wide. Heterocysts usually intercalary (Fig. 6.7d), isodiametric to longer than wide, 4.0-8.0 μm long, 4.0-7.0 μm wide.

Reproductive features. No akinetes observed. Hormogonia isopolar.

Remarks. Technically apoheterocytic (distant) development of akinetes must be seen to place the alga in the subfamily Nostocaceae, but these were not observed even in cultures approximately 1 year old. Presumably conditions on full-strength medium were not amenable to akinete formation. However the well-defined non-diffluent mucilaginous colonies are very characteristic of the genus *Nostoc* (Bourrelly 1970, Komárek and Anagnostidis 1989). The loosely grouped trichomes in colourless, formless mucilage, cell shape and size, and relatively large heterocyst are features characteristic of *N. paludosum* (Geitler 1932).

Nostoc has been reported from soils and fresh water (Bourrelly 1970). *N. paludosum* is cosmopolitan in stagnant water (Geitler 1932).

Family Rivulariaceae

***Calothrix* cf. *kossinskajae* Poljansky** Fig. 6.6b, c, j, k.

Geitler (1932) p607-609, Fig. 383 (1-4). Komárek and Anagnostidis (1989) p290-292.

Distribution. MF, SO (EC)

Vegetative features. Solitary, tapered, heteropolar trichomes, with basal heterocyst (Fig. 6.6b, c) and thin colourless sheath from above heterocyst, extending to and enveloping tapered terminus (Fig. 6.6j, k). Cells wider than long at base, to longer than wide at apex, 0.5-6.0 μm wide, 3.0-7.0 μm long. Pronounced constrictions at transverse walls.

Reproductive features: Older trichomes show evidence of meristematic zone in mid-region (Fig. 6.6k). No hormogonia observed.

Remarks. No false branching (a characteristic of the Rivulariaceae) has been observed, however this occurs during hormogonia production, a process dependent on environmental conditions (Komárek and Anagnostidis 1989), such as P supply to a

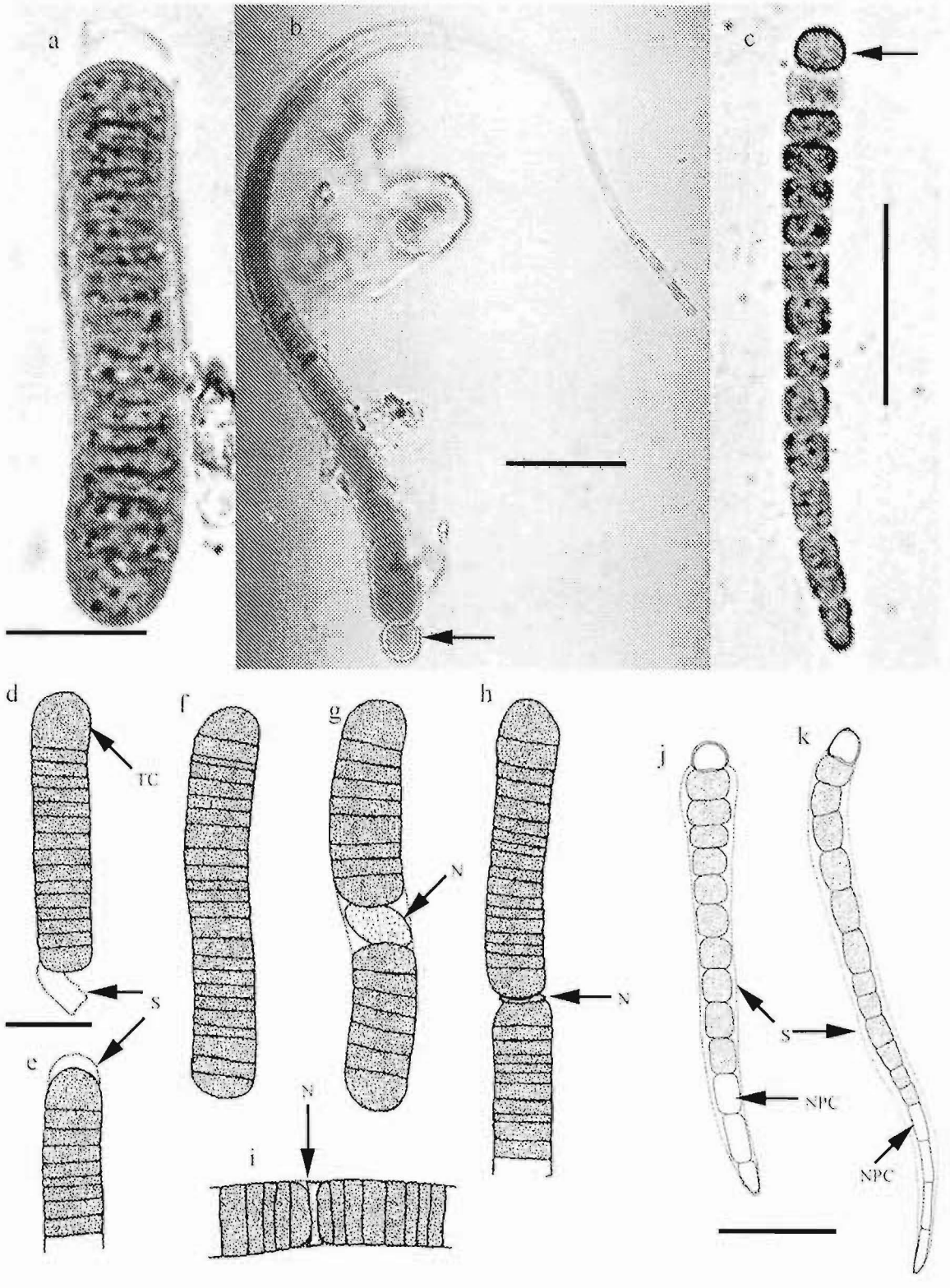


Fig. 6.6. a, d-i, *Hormoscilla* sp., enrichment cultured material: a, mature trichome; d-f, typical trichomes with large terminal cells (TC) and thin sheath (S) sometimes visible; g-i, division of trichomes via necridic cells (N).

b, c, j, k, *Calothrix* cf. *kossinskajae*, enrichment culture material: b-c, trichomes, note basal heterocyst (arrows); j-k, trichomes with non-pigmented cells (NPC) in terminal region and thin sheath (S) visible.

All scales=10 μm (use scale in d for d-i; use scale in j for j-k).

previously P-limited system (Whitton 2000), and has not been seen in the Mt Philistine specimens. Location of dividing cells suggests a subterminal meristematic zone, as reported for the Rivulariaceae. Akinetes, which are absent from most genera in the Rivulariaceae but are facultative in *Calothrix*, have also not been observed. Therefore, solitary trichomes and non-diffluent mucilage (especially at trichome terminus) are important in assigning this alga to the genus *Calothrix*. The genus *Dichothrix* is very similar to *Calothrix*, but published illustrations show diffluent mucilage surrounding the trichome (Komárek and Anagnostidis 1989). Freshwater habitats, basal thickening and width of the trichome are characteristic of *C. kossinskajae* (Geitler 1932). Its mucilage sheath more resembles *C. clavata* West (Geitler 1932), but the trichome width is too small for it to be considered this species.

C. kossinskajae was described attached to *Cladophora* in swamps near St Petersburg, Russia (Geitler 1932). It has not been included in New Zealand species lists (Cassie 1984).

Order Stigonematales

Family Fischerellaceae

***Fischerella* sp.** Fig. 6.7b, c, e-j, Fig. 6.8a-b.

Anagnostidis and Komárek (1990) p46, 50, Table 4.

Distribution. P, MF, SO, R, LV, LM, ASN (DE, EC)

Vegetative features. Main branch of trichome uniseriate to multiseriate, 18-38μm wide (Fig. 6.7b, c, f, i, Fig. 6.8a), with thick brown laminated mucilage sheath. Secondary branches uniseriate; multiseriate main branch tapering to uniseriate terminus (Fig. 6.7g, j). Terminal cells rounded. Cells oval to globose, 5-17 μm long, 12-20 μm wide, separated by single mucilage layers but sometimes with elongations of the cell wall towards adjacent cells (Fig. 6.7i). Outermost mucilage layer often thicker at terminal region of trichome, but inner layers thinner (Fig. 6.7j). Heterocysts intercalary (Fig. 6.7b).

Reproductive features. Division in three planes. Hormogonia produced by necridic cells within uniseriate secondary branches. Hormogonia initially without heterocysts,

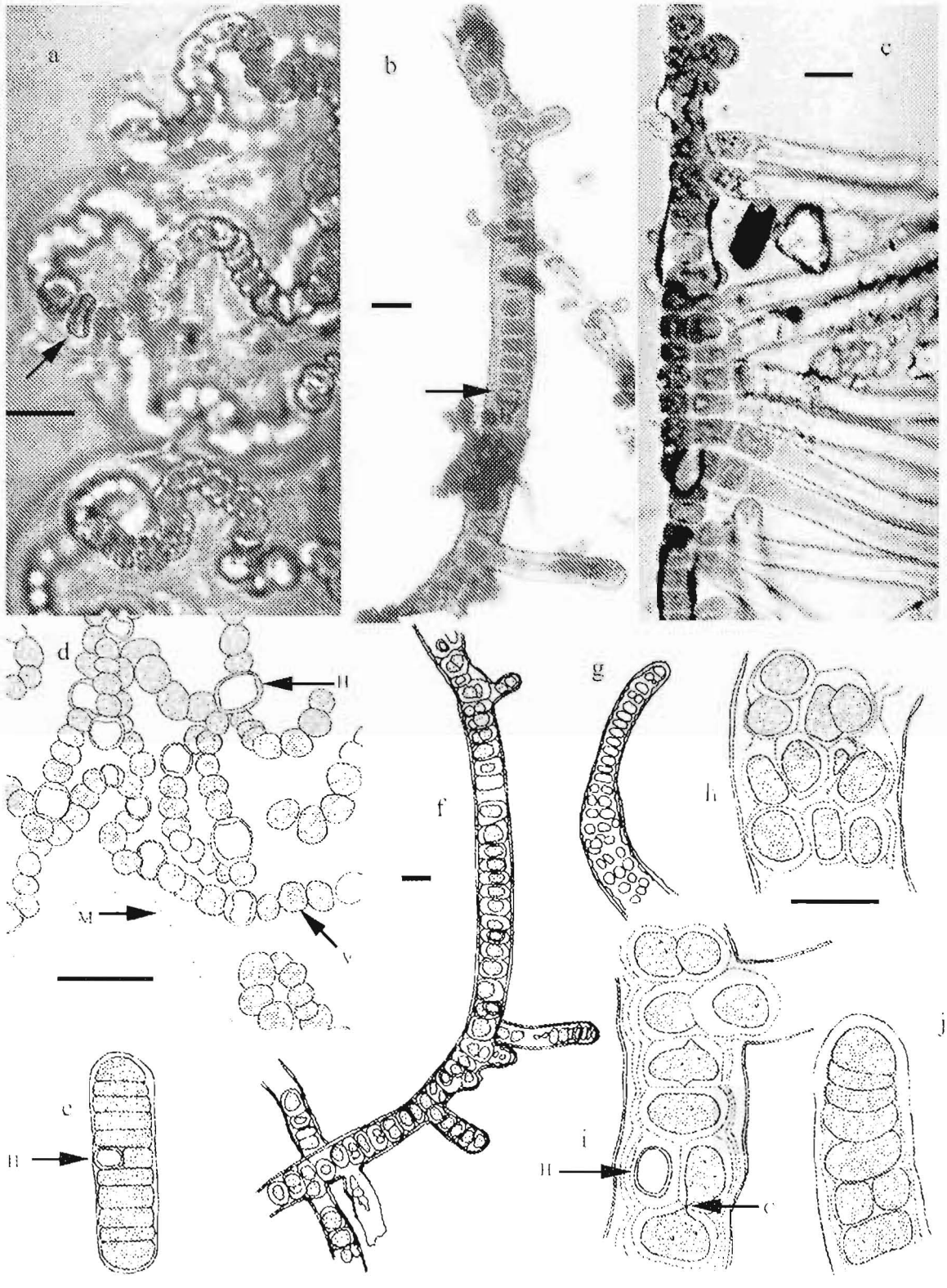


Fig. 6.7. a, d, *Nostoc paludosum*, agarised culture material: a, trichomes in mucilage showing heterocysts (arrow); d, mucilaginous colony showing heterocysts (H), mucilage (M), vegetative cells (V).

b, c, e-j, *Fischerella* sp., field material: b, branched trichome showing heterocyst (arrow); f, typical trichome; g, terminal region of trichome broadening to multiseriate section; h, detail of multiseriate portion showing individual sheaths around cells; i, detail of branched region with heterocyst (H) and connections between cells(C); j, detail of terminus showing mucilage layers; enrichment culture material: e, developing thallus; e,young thallus, note heterocyst (H).

All scales= 10 µm (use scale in f for f-g, use scale in h for e and h-j).

which develop by a lateral division and differentiation of one of the daughter cells (Fig. 6.7c, 6.8b).

Remarks. Anagnostidis and Komárek (1990) stated that many diacritical features require more research to differentiate between genera in the Stigonemataceae. However, those supporting assignment of this alga to *Fischerella* are differentiation of multiseriate main and uniseriate secondary branches, and identical thallus development following settling of hormogonia (Fig. 6.7c) as shown by Anagnostidis and Komárek (1990, Table 4). Pit connections between cells are reported to be characteristic of *Stigonema* (Van den Hoek *et al.* 1995). These structures may be indicated by the cell wall extensions observed in the Mt Philistine specimens (Fig. 6.7i).

Fischerella and *Stigonema* are reported to occur on damp rocks and in freshwater habitats (Geitler 1932, Van den Hoek *et al.* 1995). In New Zealand, *Fischerella* has been reported from Taupo, Tekoa, and Omarama soils (Cassie 1984) and from a sphagnum bog on Woolshed Hill, Arthur's Pass National Park (Croasdale and Flint 1972).

Division Euglenophyta

Class Euglenophyceae

Order Euglenales

***Euglena* cf. *pisciformis* Klebs** Fig. 6.8c, e-g.

Ettl and Gärtner (1995) p246, Fig. 62c.

Distribution. SO (DE, EC)

Vegetative features. Cells single, exhibiting typical euglenoid motility (compare Fig. 6.8e and g); 40-50 µm long, 7-12 µm wide when fully extended. Stigma anterior, free in cytoplasm (Fig. 6.8c). Chloroplasts parietal, band-shaped to discoidal, 5 or more per cell (Fig. 6.8e, f), often hard to distinguish due to cytoplasmic granulation (Fig. 6.8c). Flagella and pyrenoids not observed.

Reproductive features. None observed.

Remarks. Size and chloroplast shape are most similar to *E. pisciformis*. Although Ettl and Gärtner (1995) describe motility of this species as weak, this seems somewhat ambiguous: the pellicle of the Mt Philistine strain is clearly highly flexible, yet little

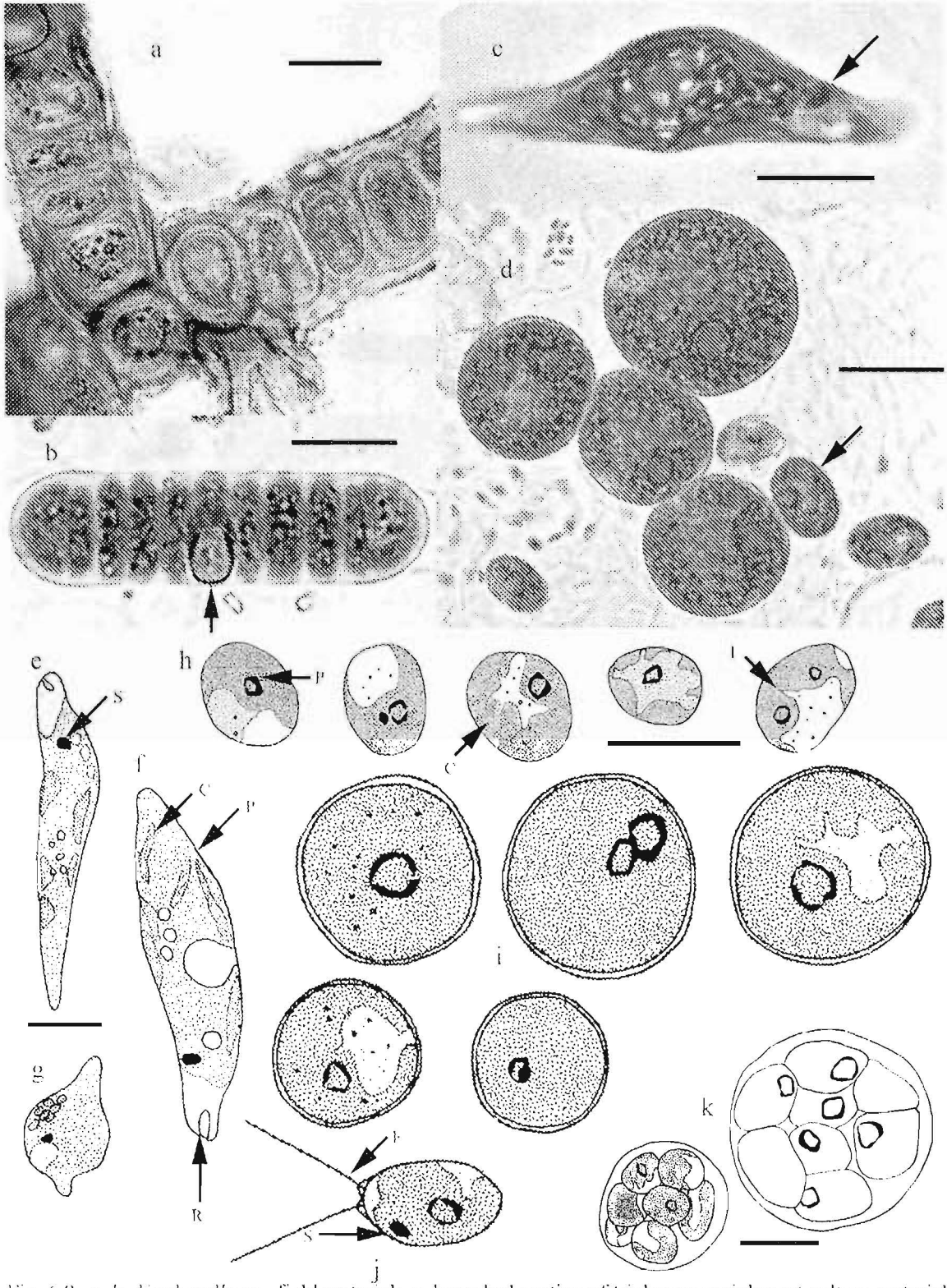


Fig. 6.8. a, b, *Fischerella* sp., field material: a, branched portion of trichome; enrichment culture material: b, young thallus (arrow indicates heterocyst).

c, e-g, *Euglena* cf. *pisciformis*, enrichment culture material: c, typical cell (arrow indicates stigma); e, f, cells in extended position (C=chloroplast, S=stigma, R=reservoir, P=flexible pellicle, V=vacuolar space); g, cell in contracted form.

d, h-k, *Chlorococcum taiwense*, agarised culture material: d, mature cells and young cells (arrow); h, young cells (C=chloroplast, I=incision in chloroplast, P=pyrenoid); i, mature cells; j, zoospore (F=flagella, S=stigma); k, autosporangia

All scales=10 µm (use scale in h for h-j).

horizontal creeping movement is observed. This situation could correspond to the published description. Other species of *Euglena* with a similar length range either have asteroidal chloroplast arrangements (*E. myxocylindrica* Bold & MacEntee and *E. geniculata* Dujardin), or are too narrow (*E. mutabilis* Schmitz).

E. pisciformis has been reported from European soils (Ettl and Gärtner 1995).

Division Chlorophyta

Class Chlamydophyceae

Order Chlamydomonadales

Family Chlamydomonadaceae

***Chlainomonas kolii* (Hardy & Curl) Hoham** Fig. 6.9-6.12.

Hoham (1974a) p394, Fig. 2-9. Hoham (1980), Fig. 1.

Distribution. SN (DE)

Vegetative features. Cells spherical to ellipsoidal, (15-) 20-30 μm long, (10-) 15-22 μm wide, contents masked by red secondary pigment. Colourless area 1-5 μm wide separates cell membrane from "wall structure" (Hoham 1980), composed of two outer envelopes (Fig. 6.11b, g, h, i, 6.9a-c, u). Inner envelope smooth, approximately equidistant from cell throughout; outer envelope appearing ornamented with regular notched pattern in LM (Fig. 6.9a), lying against inner envelope except at cell anterior where it forms a collar or funnel (Fig. 6.9k-r, u), often slightly offset from longitudinal axis, and where ornamentation is most apparent. Papilla-like structure occasionally observed at cell anterior inside the envelopes (Fig. 6.9h). Four flagellar grooves (Fig. 6.9b, u) extend from cell through colourless area at cell anterior. Flagella very rarely observed, 2-4 per cell (Fig. 6.9f, g, s). Outer envelope shed in older cells (Fig. 6.9.h-i), inner envelope and flagellar grooves retained (Fig. 6.10a-c, g-n). TEM shows outer envelope to be composed of layered material (Fig. 6.11f, j-l), and the chloroplasts to be numerous and discoidal (possibly parietal in living cells), surrounding a central nucleus (Fig. 6.11e). SEM shows outer envelope to have a network structure (Fig. 6.9j).

Reproductive features. Zoospores, approximately 18 μm long, 10 μm wide, biflagellate, 2-8 per sporangium (Fig. 6.10e, f, o), identical with the description of *Chloromonas rubroleosa* cells in field samples (i.e. without internal structures visible), but produced

from sporangium with reticulate collar. Very rarely observed (3 examples in over 500 examined samples in which the collared cells were common).

Remarks. The outer envelope is the critical feature in confirming that this organism is *Chlainomonas kolii* as described from North America. Hoham (1980) has shown that this envelope in the American algae is a reticulate, net-like structure when viewed in SEM. The limited observations (Fig. 6.9j) of this envelope structure in New Zealand cells confirms the identification. In TEM the outer envelope appears to be made of layers of material which "flake" from the envelope. There is some evidence that loss of this envelope in the Mt Philistine cells occurs at low levels of NH_4-N in snow (see Chapter 4, snow ecology).

Hoham (1974a) reported one axial chloroplast in North American *C. kolii*, whereas Mt Philistine specimens contain numerous discoidal chloroplasts surrounding the nucleus. Numerous parietal chloroplasts were noted in the original description of the species as *Trachelomonas kolii* (Hardy and Curl 1968); possibly, these could have been mistaken for a single asteroidal chloroplast by Hoham (1974a). Another difference is that North American cells, having lost the external envelope, have a papilla-like apex at the cell anterior, a structure absent from the New Zealand cells, although various blunt protruberances have been observed (Fig. 6.10b). Flagellated cells have also been very rarely observed, and have not yet been seen on living specimens, whereas Hoham (1974a) reported a two-week period of motility in the laboratory following collection. These apparent differences in morphology may be explained by the different conditions common in Mt Philistine snow compared to those in forested North American snowpacks (see Chapter 4: snow ecology).

Cell division has not been reported in the North American strain, and Hoham (1974) considered that "there is a remote possibility that the quadriflagellate organism is a prolonged planozygote rather than a vegetative cell". Cell division in the New Zealand collared cell was very rarely observed. The daughter cells found in incubated snowmelt appear the same as *Chloromonas rubroleosa*, suggesting that these cell types may form part of a complex life cycle. A proposed life cycle based on the information so far obtained is presented in Fig. 6.12.

The evidence that the two Mt Philistine taxa, *Chloromonas rubroleosa* and *Chlainomonas* cf. *kolii*, are the same organism is as follows. What is apparently cell division has been observed within the collared cells (Fig. 6.12:5) on rare occasions, and the daughter cells have the same external morphology as *Chloromonas rubroleosa* (Fig.

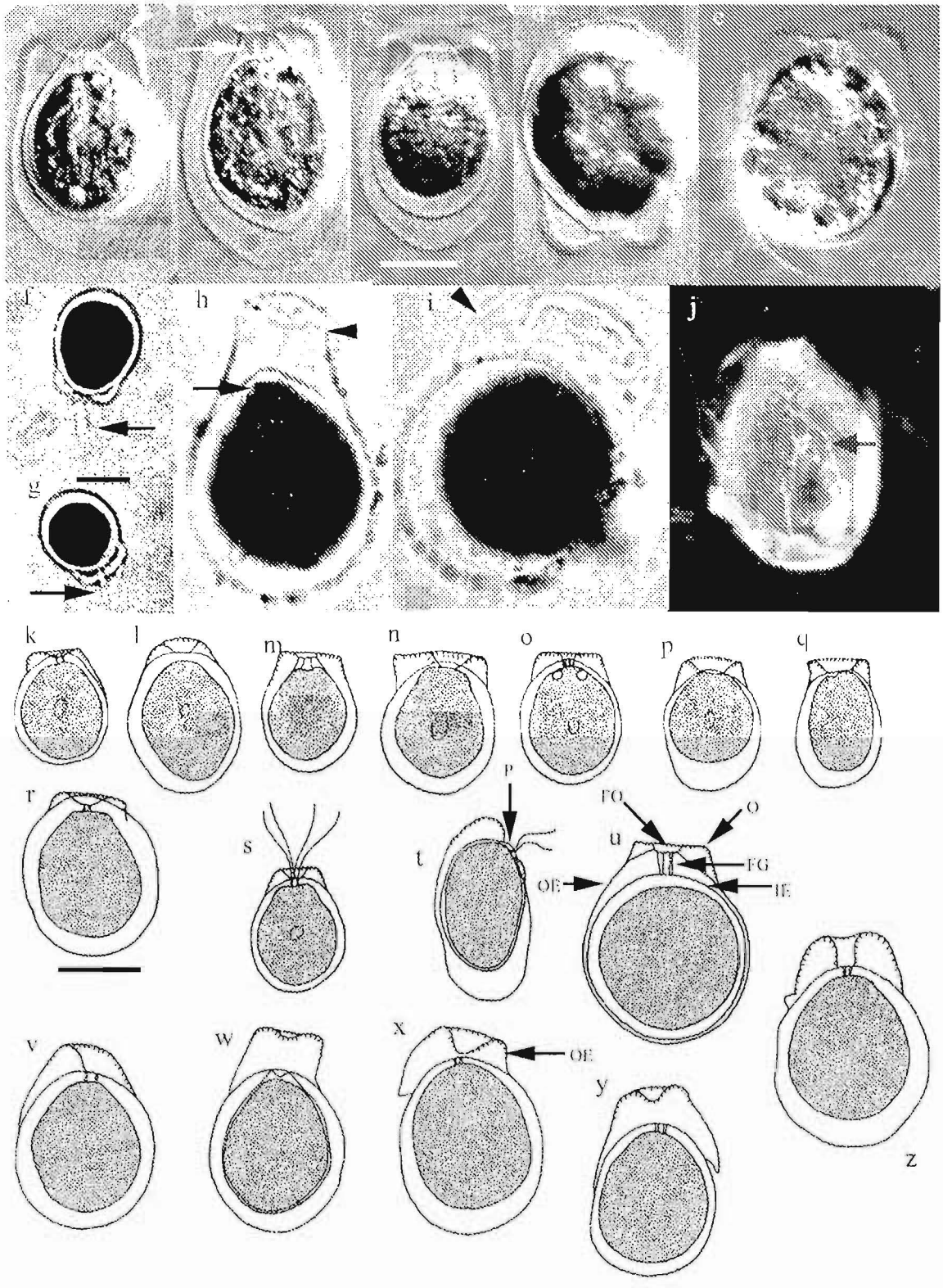


Fig. 6.9. *Chlainomonas kolii*, field material: a-e, Nomarski DIC showing ornamented outer envelope (arrowhead) and collar with flagellar grooves (arrow); f, g, rare cells with flagella (arrows), seen in counting chamber; h-i, loss of outer envelope (arrow in h shows papilla-like structure, arrowheads to outer envelope being lost); j, SEM of cell showing reticulate outer envelope (as shown by Hoham 1980); k-r, typical preserved cells lacking flagella; s, rare quadriflagellated cell; t, biflagellated cell with ornamentations and papilla (P); u, live spherical cell (FO=flagellar opening, OE=outer envelope, IE=inner envelope, O=ornamentations; FG=flagellar grooves); v-z, cells losing outer envelope (OE).

All scales=10 μm (use scale in c for a-e, h-j, g for f-g, r for k-z).

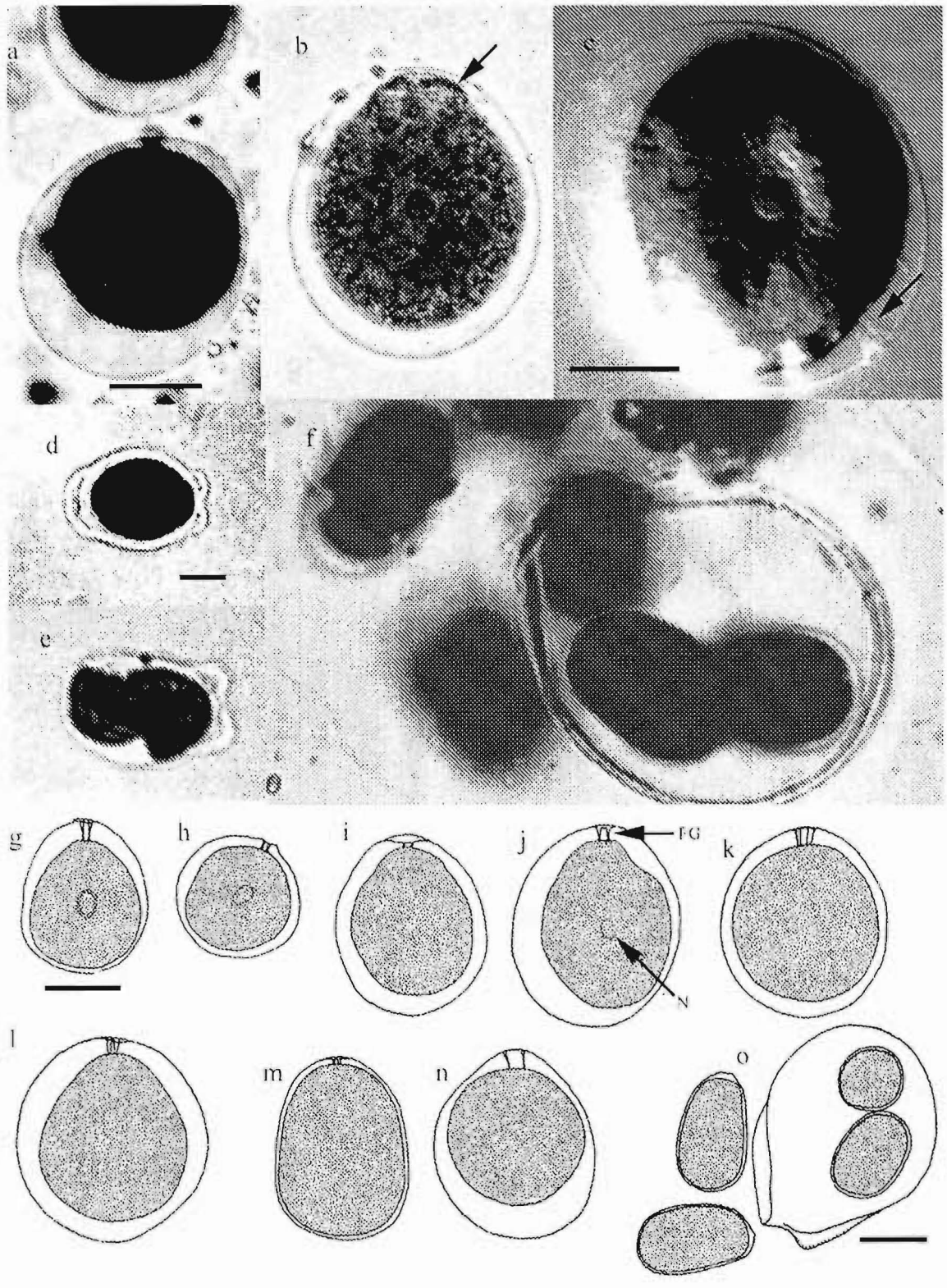


Fig. 6.10. *Chlainomonas kolii*, field material: a, living cells lacking outer envelope; b, preserved specimen showing apical bulge caused by wall deformation (arrow); c, Nomarski DIC of preserved cell showing flagellar grooves (arrow); d, cell with two collars seen in counting chamber; e, cell division seen in counting chamber; f, release of cells superficially identical with *Chloromonas rubroleosa* (Fig. 6.11); g-l, preserved cells showing flagellar grooves (FG) and nucleus (N); m, n living cells showing variation in envelope; o, release of daughter cells from collared sporangium.

All scales=10 μm (use scale in a for a, b, f; d for d, e; g for g-n).

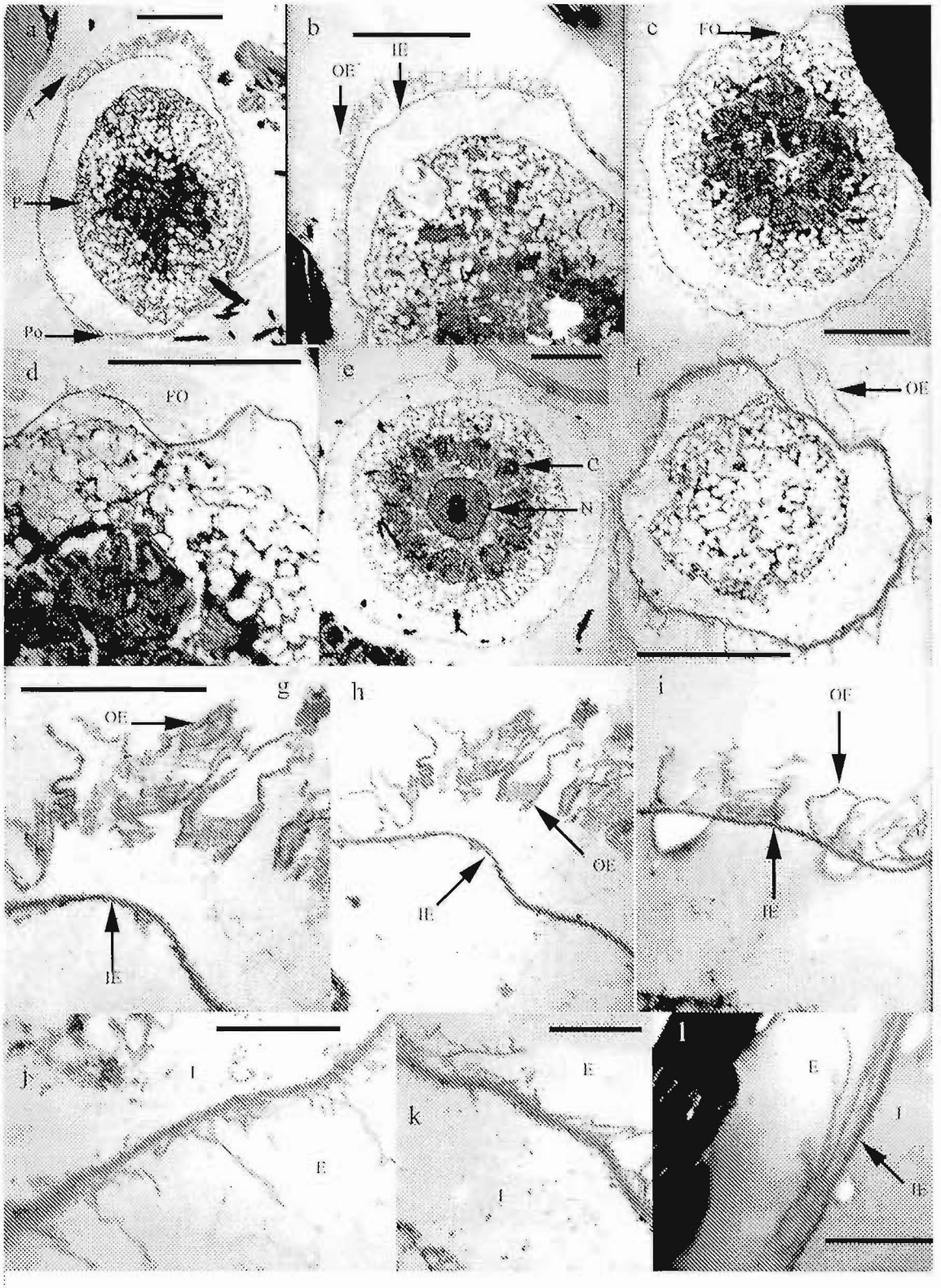


Fig. 6.11. *Chlainomonas kolii*, TEM of field material: a, longitudinal section of cell (A=anterior, Po=posterior, P=protoplast); b, section through collar region (OE=outer envelope, IE=inner envelope); c, section showing flagellar opening (FO) in collar; d, detail of this region; e, median, transapical section showing large central nucleus (N) and surrounding chloroplasts (C); f, tangential section showing exfoliation of outer envelope layers; g-h, detail of section through collar region; i, detail of section through flank of cell where envelopes are joined; j-l, detail of envelopes in region of cell posterior (I=interior of cell, E=exterior to cell, IE=inner envelope, OE=outer envelope).

Scale bars: a-f=5 µm, g-k=1 µm, l=0.5 µm.

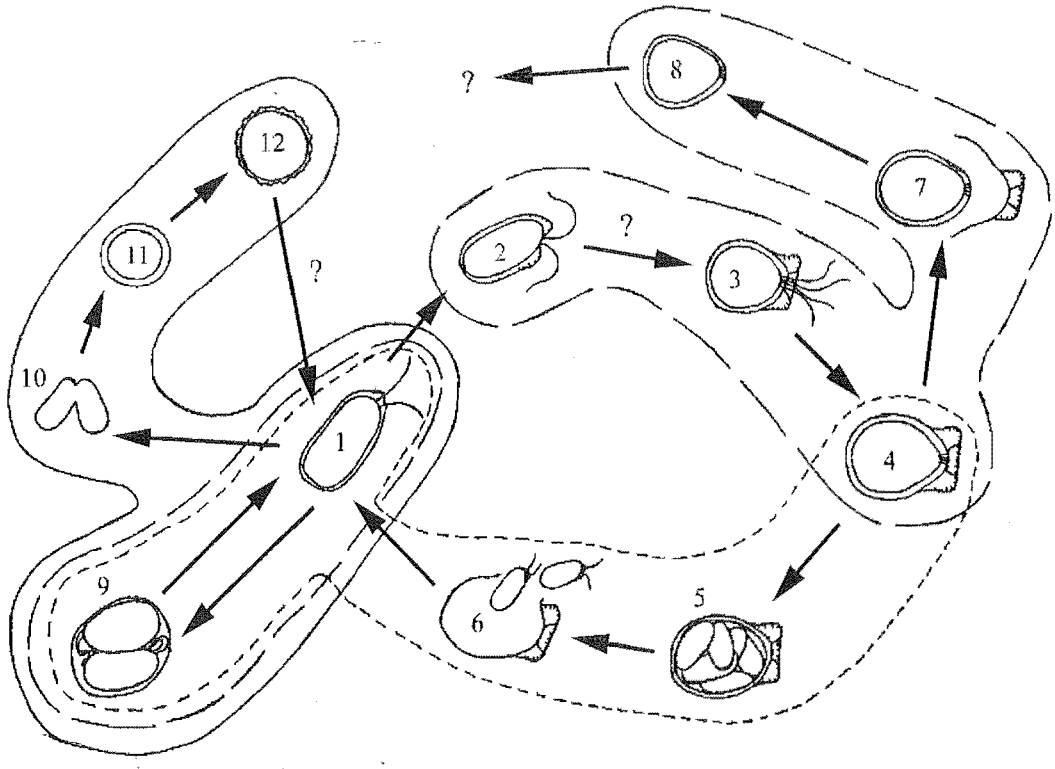


Fig. 6.12. Proposed life cycle for *Chlainomonas kolii* from Mt Philistine based on the information obtained from three summer seasons.

= seen in liquid culture.

= seen in field samples.

= seen in incubated snowmelt.

1 = biflagellate vegetative cells, apparently identical to *Chloromonas rubroleosa* (see Fig. 6.11a-d).
2 = biflagellate cell developing ornamented collar (only one example seen, see Fig. 6. 14t).
3 = *Chlainomonas kolii* quadriflagellate cell (rarely observed, see Fig. 6.14f, g, s).
4 = *C. kolii* cell type lacking flagella (most common cell observed, see Fig. 6.14a-e).
5 = asexual zoosporangium formed from *C. kolii* cell (very rarely observed, see Fig. 6.15e, f, o).
6 = release of daughter cells (see Fig. 6.15f, o).
7 = loss of outer envelope by *C. kolii* cell (see Fig. 6.14u-z).
8 = *C. kolii* cell lacking outer envelope (see Fig. 6.15a-c).
9 = asexual sporangium produced from *Chloromonas rubroleosa* type cells (see Fig. 6.11e-h).
10 = sexual fusion in *Chloromonas rubroleosa* type cells (see Fig. 6.11j-l).
11 = zygote (not illustrated elsewhere).
12 = resting cyst thought to be produced by sexual fusion in *Chloromonas rubroleosa* type cells (see Fig. 6.11i), possibly produces type 1 cells.

? above arrow: link between two states only hypothetical (not actually observed)

? = next link in cycle not yet determined.

6.12:1). The infrequent occurrence of this cell division is accompanied by very low concentrations of *Chloromonas rubroleosa* in field samples (see Chapter 4). The bimammillate papilla of *Chloromonas rubroleosa* is offset from the longitudinal axis of the cell, as is the collar surrounding the cell anterior of *Chlainomonas* cf. *kolii*. One observed cell (Fig. 6.9t, upper left) from a preserved sample appears to represent a transition between the two cell types, having an offset papilla, two flagella and (apparently) a developing ornamented collar (Fig. 6.12:2). The chloroplasts of both cell types are numerous and discoidal, surrounding a central nucleus. Although the chloroplasts of *Chlainomonas kolii* in TEM appear to be sub-parietal (Fig. 6.11e), whereas those of *Chloromonas rubroleosa* are parietal (Fig. 6.11t, u), this could be a difference between cultured and field material. The identity of any resting cyst of the New Zealand *Chlainomonas kolii* is uncertain, but that of *Chloromonas rubroleosa* (Fig. 6.11i, 6.12:12), which is rarely observed in older cultures, closely resembles Hoham's observations of the resting cyst of *Chlainomonas kolii* in North America.

Culturing of *Chloromonas rubroleosa* has not yet resulted in the production of any collared cells. The product of sexual reproduction in *Chloromonas rubroleosa* appears to be a spherical zygote leading to the development of a resting cyst. It is possible that the cells released following division of the *Chlainomonas* collared cell are actually distinct from *Chloromonas rubroleosa*. Until conclusive evidence is produced using cultures, the evidence linking the two is inadequate to combine them into a single species.

Chlainomonas kolii has previously been reported from snowpacks beneath forest canopies in North America (Hoham 1974a). It has not been found elsewhere prior to this study. It occurs in at least two New Zealand sites: Mt Philistine and old snow in a tributary of the Eglinton Valley, Fiordland.

cf. *Chlamydomonas* Fig. 6.14b, e.

Kol (1968b) Tafel IV: 16, 21, VII: 2. Marchant (1982) Fig. 1.

Distribution. SN, ASN?, A, P, LM, LV, MF, R (DM)

Features. Cells spherical to very broadly ellipsoidal, 16-25 μm diameter, often surrounded by an envelope (Fig. 6.14e). Contents masked by dense red pigment,

sometimes localised towards cell centre (Fig. 6.14e, lower two cells). Cells often obscured by adhering mineral material.

Reproductive features. None observed. Probably a resting cyst of a flagellated snow alga.

Remarks. These cells resemble one of many cell types attributed in the past to *Chlamydomonas nivalis* (Kol 1968b), the most commonly reported snow alga in the Northern Hemisphere. It has not been shown that all these cell types belong to the same species (Thomas and Broady 1997). This organism (or cells morphologically identical) has been found extensively in the Mt Cook snow flora, where it forms blooms of red snow. It has not been found in such abundance on Mt Philistine, although it is clearly dispersed across a range of habitats. It may be present on Mt Philistine solely as aerobiota (see Chapter 5). Mineral material adhering to the cells gives them the same appearance as those recorded in Kosciusko National Park, Australia (Marchant 1982).

This alga has probably been reported from New Zealand previously as *Chlamydomonas* sp. (Thomas and Broady 1997) and *C. nivalis* (Wilson 1976).

***Chlamydomonas* cf. *culleus* Ettl** Fig. 6.13c, j-l.

Ettl and Gärtner (1995) p274-275, Fig. 68c.

Distribution. MF, SO, P, LM (DE, EC, MC)

Vegetative features. Cells ellipsoidal to slightly pyriform; 6.5-8.0 μm long by 4.0-5.0 μm wide; flagella ~5 μm long. Chloroplast parietal, extensive, cup-shaped, with 1-6 incisions of varying depth (Fig. 6.13j, k). Pyrenoid single (rarely 2), lateral. Papilla conical. Stigma elliptical, commonly present in chloroplast anterior.

Reproductive features. Zoospores, 2-4-8 per sporangium (Fig. 6.13l), 5-7 μm long, 3-4 μm wide.

Remarks. Single lateral pyrenoid, chloroplast shape and pattern of incisions, presence of papilla, cell size and anterior stigma make this alga most similar to *C. culleus*. However the published description (Ettl and Gärtner 1995) shows a broader papilla than on the Mt Philistine cells, the incisions in the chloroplast are narrower and less variable, and the cells appear slightly more pyriform.

C. culleus has been reported from soils in Czechoslovakia (Ettl and Gärtner 1995). This species is not included in New Zealand species lists (Cassie 1984).

***Chlamydomonas* cf. *moewusii* Gerloff** Fig. 6.13a, b, e-i.

Ettl and Gärtner (1995) p266, 268, Fig. 66m.

Distribution. P, MF, SO, ML, HL (MC)

Vegetative features. Palmelloid colonies (Fig. 6.13h) dominate on agarised medium. Cells cylindrical to ellipsoidal, 10-17 μm long, 6-10 μm wide. Flagella 15 μm long arising from small conical apical papilla (Fig.6.13e). Chloroplast parietal, cup-shaped, open at anterior end, with 1 or more small incisions or perforations (Fig. 6.13g). Pyrenoid single (rarely 2), with perforated starch sheath. Stigma small, elliptical, anterior, only occasionally observed. Contractile vacuoles anterior. Granules accumulate in central cytoplasm against chloroplast surface.

Reproductive features. Zoospores 7-10 μm long, 4-8 μm wide, 2-4-8 per sporangium. Zoospores are parallel inside isolated zoosporangia (Fig. 6.13i), but more irregular in sporangia within palmelloid colonies (Fig. 6.13h).

Remarks. Size, chloroplast shape and perforations/incisions, lateral pyrenoid, and single papilla place the alga in *C. moewusii* (Ettl and Gärtner 1995). However, the stigma is only sometimes observed and papilla is conical rather than "keel"-shaped. It may be separated from the nearest alternative (*C. planoconvexa* Lund) because the Mt Philistine strain has no dorsiventral polarity and has a distinct papilla. Predominance of palmelloid colonies in culture in suboptimal growth conditions has been reported for other Chlamydomonadacean flagellates on agarised medium (e.g. Hoham 1980).

C. moewusii is a cosmopolitan alga often found in soils (Ettl and Gärtner 1995). A variety of this species (*C. m.* var. *microstigmata* (Lund) Ettl) has been found in Temuka soil in New Zealand (Sarma and Chapman 1975).

***Chlamydomonas* cf. *noctigama* Korschikoff in Pascher** Fig. 6.13d, m-q, 6.14a, d.

Ettl and Gärtner (1995) p275, Fig. 68f.

Distribution. SO, MF, LV, LM (MC)

Vegetative features. Occurs mainly as palmelloid colonies or single cells lacking flagella when grown on agarised medium. Cells broadly ellipsoidal, 21-25 μm long, 12-16 μm wide. Chloroplast parietal, cup-shaped, open at anterior end, with numerous small to large perforations. Pyrenoid large (Fig. 6.13d, m), lateral, sometimes not

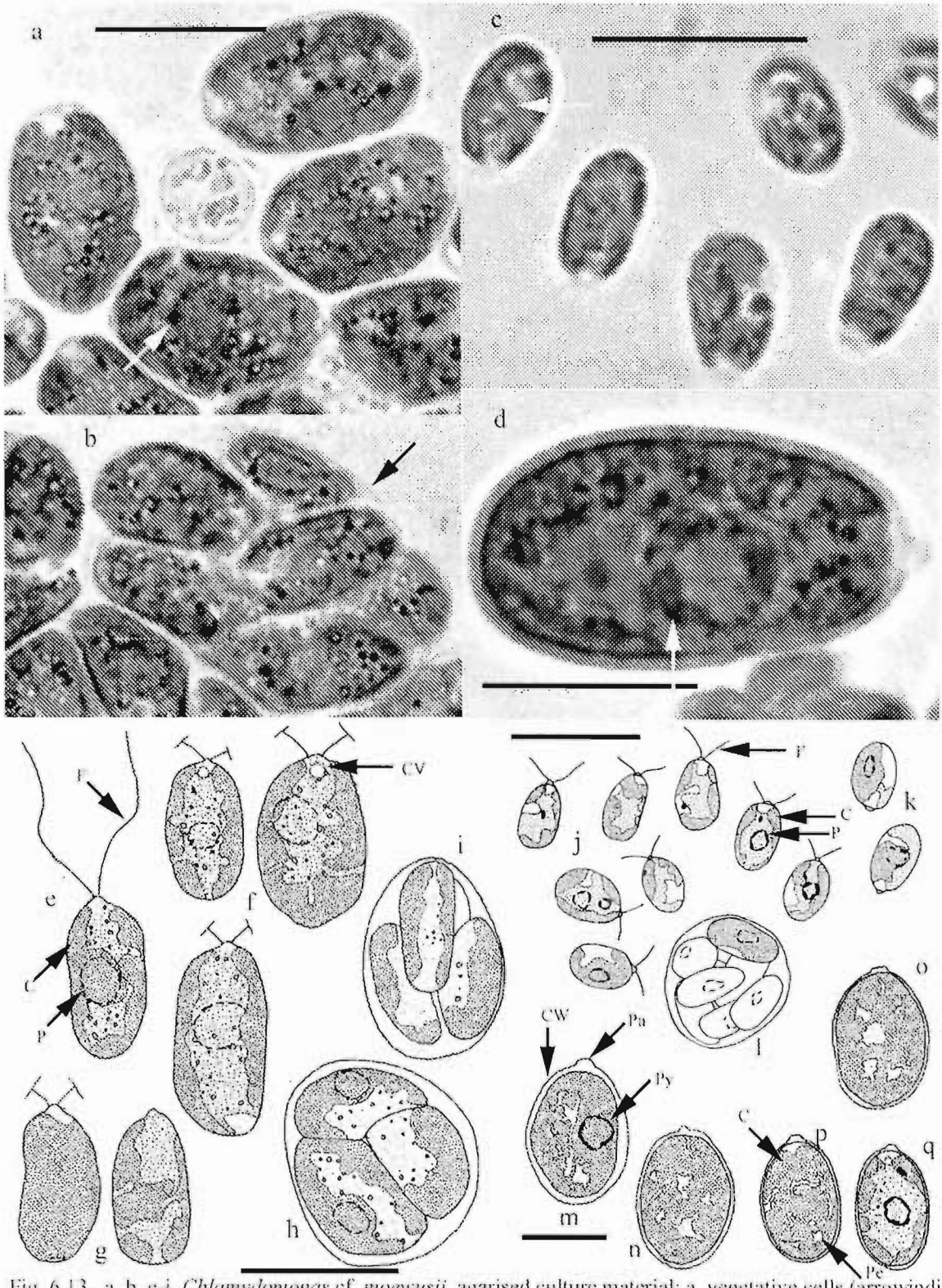


Fig. 6.13. a, b, e-i, *Chlamydomonas* cf. *moewusii*, agarised culture material: a, vegetative cells (arrowindicates pyrenoid); b, sporangium in palmelloid colony(arrow indicates sporangium wall); e, vegetative cell with full-length flagella (F) shown (C=chloroplast, P=pyrenoid); f, motile vegetative cells (flagella shown truncated, CV=contractile vacuole); g, two surface views of chloroplasts; h, sporangium in palmelloid colony; i, zoosporangium.

c, j-l, *Chlamydomonas* cf.*culleus*, field material: c, group of cells (arrow indicates pyrenoid); j, motile vegetative cells (F=flagella, C=chloroplast, P=pyrenoid); agarised culture material: k, cells showing clearly lobed chloroplast; l, zoosporangium.

d, m-q, *Chlamydomonas* cf. *noctigama*, agarised culture material: d, vegetative cell (arrow indicates pyrenoid); m, vegetative cell showing thick cell wall (CW), papilla (Pa); n, o, vegetative cells with papillae in alternative orientations; p, surface and optical section views of chloroplast (C=chloroplast, Pe=perforation).

All scales=10 µm (use scale in a for a-b, h for e-h, j for j-l, m for m-q).

visible unless stained with iodine due to heavy granulation of chloroplast. Stigma elliptical, always anterior (Fig. 6.13q). Contractile vacuoles anterior. Papilla broad, keel-form. Cell wall thick and smooth (Fig. 6.13m).

Reproductive features. Zoospores, 16-23 μm long, 9-13 μm wide, 2-4 per sporangium (Fig. 6.14d), released by rupture of sporangium wall (Fig. 6.14e).

Remarks. Cell size, single lateral pyrenoid, shape of chloroplast, and keel-like papilla all support assignment to *C. noctigama.* However according to Ettl and Gärtner (1995), the chloroplast should contain radial incisions, rather than perforations. Also, the stigma should not be located in the anterior of the chloroplast; however Ettl and Gärtner (1995) illustrate a cell with a clearly anterior stigma. The papilla in their illustrations is bimammillate, whereas the upper surface of the papilla in the Mt Philistine specimens is flat. The nearest alternative, *C. chlorococcoides* Ettl & Schwarz, is excluded on the basis of a half-spherical papilla and a divided chloroplast (Ettl and Gärtner 1995). Morphology of the zygote cell wall can also distinguish these two species, but zygotes were not observed.

C. noctigama has been reported from mountain soils in Europe (Ettl and Gärtner 1995). The species is not included in species lists from New Zealand (Cassie 1984).

***Chloromonas* cf. *rosae* var. *polychloris* Ettl** Fig. 6.14c, f-p.

Ettl (1970) p 144-145, 270-271, Fig. 45:1.

Distribution. SO, LM, LV (MC)

Vegetative features. Palmelloid colonies (Fig. 6.14n-o) dominate on agarised medium. Cells ellipsoidal-cylindrical to ellipsoidal, 10-14 μm long, 5-8 μm wide. Flagella ~10 μm long arising from single wide apical papilla (Fig. 6.14b, m). Chloroplasts parietal, discoid to band shape, 2-7 per cell (Fig. 6.14f-l). Stigma elliptical, frequently anterior (Fig. 6.14j). Contractile vacuoles present at cell anterior.

Reproductive features. Zoospores, 7-9 μm long, 4-5 μm wide, 2-4-8-16 per sporangium (Fig. 6.14p).

Remarks. The single broad papilla, cylindrical-ellipsoidal shape, and more than one chloroplast per cell assign the alga to *C. rosae. C. rosae* var. *polychloris* is closest because the chloroplasts are clearly separate and the papilla is broad, although it appears broader than in the illustrations of Ettl (1970).

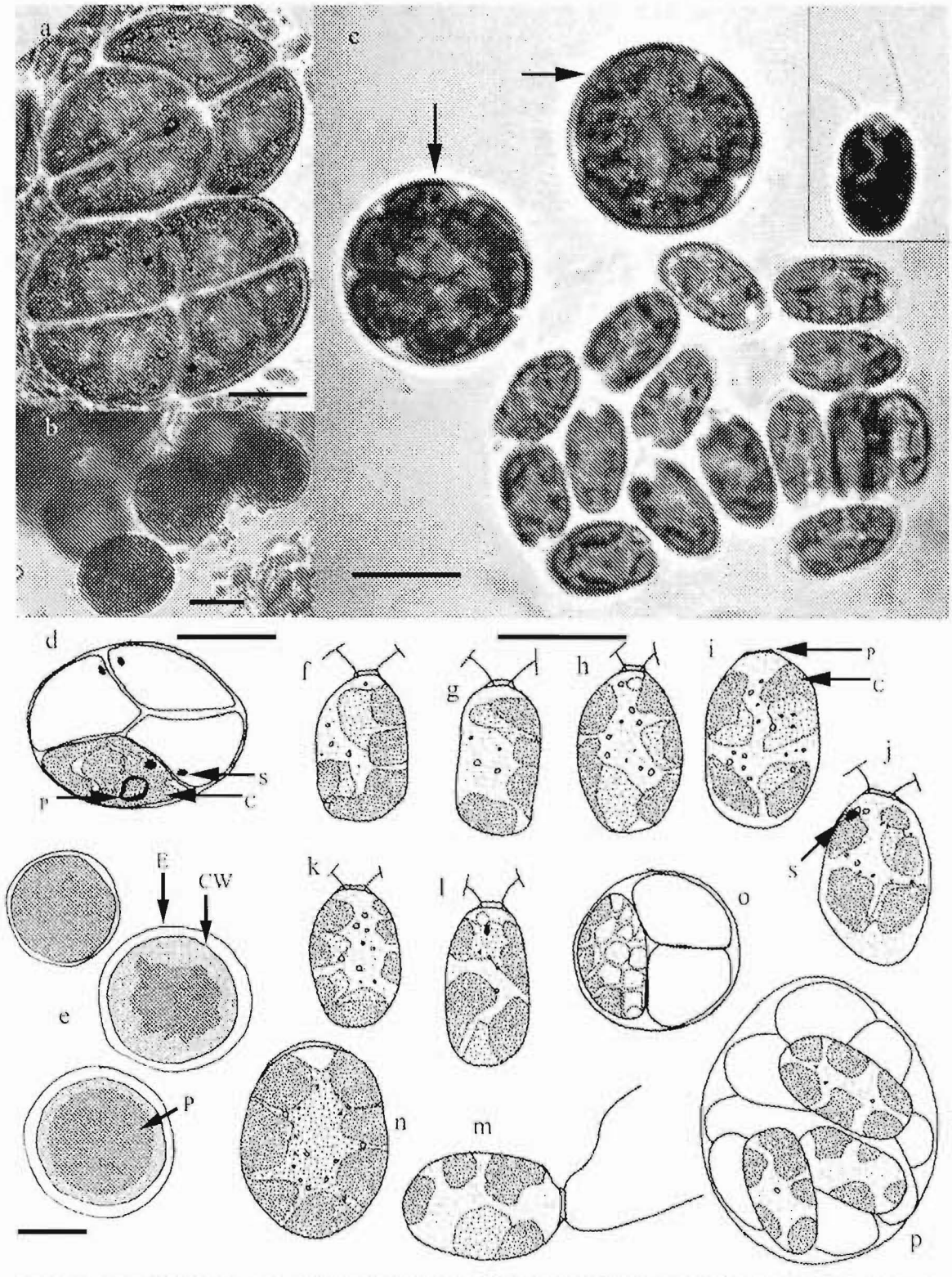


Fig. 6.14. a, d, *Chlamydomonas* cf. *noctigama*, agarised culture material: a, sporangium; d, sporangium showing stigma (S), pyrenoid (P), and chloroplast (C) of one daughter cell.

b, e, cf. *Chlamydomonas*, field material: b, group of cells in snow suspension; e, cells showing envelope (E), cell wall (CW) and densely pigmented centre (P).

c, f-p, *Chloromonas rosae* var. *polychloris*, agarised culture material: c, vegetative cells and zoosporangia (arrow; inset shows preserved flagellated vegetative cell); f-l, biflagellate vegetative cells (flagella shown truncated, C=chloroplasts, S=stigma, P=papilla); m, vegetative cell with full length flagella; n, typical cells in palmelloid colony with rounded shape and absence of papilla; o, sporangium in palmelloid colony; p, zoosporangium.

All scales=10 µm (use scale in d for d-e, h for f-p).

Ch. rosae var. *polychloris* has been reported from rainpuddles in European woodlands (Ettl 1970). It is not included in New Zealand species lists (Cassie 1984).

***Chloromonas rubroleosa* Ling & Seppelt** Fig. 6.15.

Ling and Seppelt (1993).

Distribution. SN (DE, EC, MC)

Vegetative features. Field specimens cylindrical with rounded ends; 20-23 μm long by 10-13 μm wide; cell contents obscured by red carotenoid pigment (Fig. 6.15a, b, g, h, j, l, m-s). Cultured cells cylindrical with rounded ends to ellipsoidal (to slightly pyriform); 20-29 μm long by 15-20 μm wide; central core of red pigment, possibly surrounding nucleus (Fig. 6.15c, t). Chloroplasts green, discoidal, numerous, closely packed at periphery of protoplast (Fig. 6.15c, d, t, u). Flagella arising from apically offset bimammillate papilla. With age, flagella often lost.

Reproductive features. Zoospores, 18-25 μm long by 10-16 μm wide, 2-4 per sporangium in cultured cells (Fig. 6.15f, x-aa). Cell division begins by rotation of apical region to lateral position (Fig. 6.15w). First division plane may be oblique or perpendicular to long axis of cell (Fig. 6.15x). Sexual reproduction possibly observed, with gametes fusing at anterior or posterior poles (Fig. 6.15j, k) in cultures >1 year old (also once in field material, Fig. 6.15l), resulting in spherical cells and ultimately a resting cyst. Cyst ellipsoidal to spherical, 20-25 μm long, 15-25 μm wide, cell wall thick, surface covered with numerous translucent blunt protuberances (Fig. 6.15i).

Remarks. Size range and chloroplast features are very close to those reported for *C. rubroleosa* (Ling and Seppelt 1993). Papilla shape and position, favoured growth temperature of 1-4°C, slow growth in culture and red pigment are also common features. However, cells described by Ling and Seppelt (1993) contained clearly visible nuclei and contractile vacuoles, neither of which have been seen in the present cells. Ling and Seppelt (1993) did not observe any resting cysts of *Chloromonas rubroleosa*. Flagella have not been observed in cell fusion processes (Fig. 6.15j, k), thought to be sexual reproduction, unlike in studies of some other chlamydomonadaceans (e.g. Hoham *et al.* 1997). Cell fusion also occurs at posterior ends as frequently as at anterior ends. This variable type of fusion was described in *Chlamydomonas nivalis* by Kawecka and Drake (1978). Because flagella are lost within a few minutes when these algae are

observed, even on a cold stage, it is possible that flagella are involved in initiating the process but are quickly lost once the cells become fused. Hoham *et al.* (1997) also illustrated several different cell fusion patterns in sexual reproduction of the snow alga *Chloromonas* sp-D.

It is not certain that the specimens assigned to *Chloromonas rubroleosa* from Mt Philistine exist independently of *Chlainomonas kolii* (Hardy and Curl) Hoham (evidence is presented in discussion of the latter organism, and see Fig. 6.12). Although this could suggest that *Chloromonas rubroleosa* described from the Windmill Islands, Antarctica (Ling and Seppelt 1993) is also part of a more complex life cycle including *Chlainomonas kolii* cell types, the algal flora of the Windmill Islands is well-characterised (Ling and Seppelt 1990, 1993, 1998a, b, 2000), and *C. kolii* is not known to occur. The Antarctic *C. rubroleosa* is also dominant in field samples of red snow (Ling and Seppelt 1993), whereas Mt Philistine red snow only rarely contains these cells. If the Mt Philistine cells can be linked with *C. kolii*, it is therefore more likely that the cells described here and *Chloromonas rubroleosa* from the Windmill Islands are separate species.

C. rubroleosa was originally reported causing blooms of red snow on the Clark, Bailey and Mitchell Peninsulas, Antarctica (Ling and Seppelt 1993). It has not been found previously in New Zealand.

***Chloromonas* sp. 2** Fig. 6.16a, b, g-q.

Hoham (1975) p217, Fig. 4-9. Ettl (1970) p 117-118, Fig. 33:2.

Distribution. SN (DE, MC)

Vegetative features. Cells ellipsoidal to slightly pyriform, 15-19 µm long by 7-12 µm wide. Large clear space in apical region containing 2 contractile vacuoles (Fig. 6.16h); swollen apical dome present (Fig. 6.16j). Chloroplast parietal, extensive cup-shaped, with small perforations (Fig. 6.16g-n). Stigma anterior (Fig. 6.16l), not always visible.

Reproductive features. Zoospores 8-13 µm long by 4-10 µm wide; 2-4-8 per sporangium (Fig. 6.16b, o-q). Division occurs by rotation of clear apical region to lateral position (Fig. 6.16o) and formation of transapical division plane (Fig. 6.16p). Subsequent division occurs in apical plane (Fig. 6.16q).

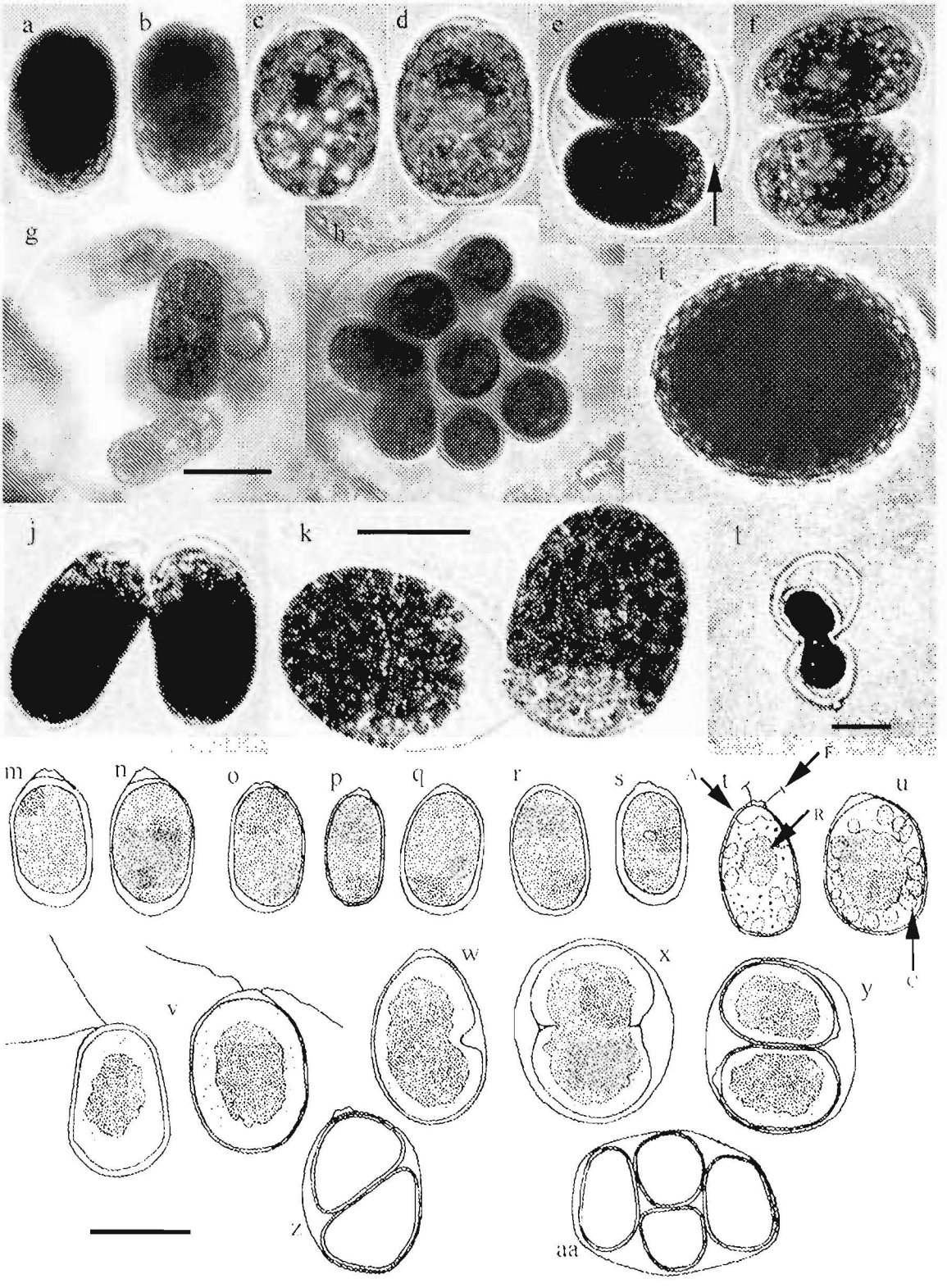


Fig. 6.15. *Chloromonas rubroleosa*, incubated snowmelt material: a, b, vegetative cells (note dark red pigment); e, g, h, zoosporangia (arrow indicates flagella of one daughter cell); i, resting cyst in 1 year old melt(note thick wall and blunt protruberances); j, apparent sexual fusion. Liquid culture material: c, d, vegetative cells (note more rounded shape, reduced pigment and visible chloroplasts); f, zoosporangium; k, apparent sexual fusion; t, u, vegetative cells (F=flagella, R=red pigment surrounding nucleus, C=chloroplasts, A=apical clear region); v, preserved cells showing flagella; w-y, cell division process, culminating in 2-celled zoosporangium; z, sporangium retaining papilla; aa, zoosporangium with 4 spores arranged in 2 pairs aligned at 90 degrees to one another. Field material: l, apparent sexual fusion (seen in counting chamber).

All scales 10 μm (use scale in k for a-f, i-k, use scale in g for g-h).

Remarks. A swollen apical dome, rather than true papilla, cell size, and ellipsoidal shape are common features with *Chloromonas pichinchae* (Lagerheim) Wille. However, Hoham (1975) does not illustrate perforations of the chloroplast or a stigma. Also, no zygotes or quadriflagellate stages have been confirmed from the Mt Philistine cells. The closest species assignment according to Ettl (1970) is *C. clathrata*, due to chloroplast perforations, ellipsoidal shape, relatively thick membrane and anterior stigma. However, *C. clathrata* has been reported from soils and lakewater, so clearly has a differing ecology.

***Chloromonas* sp. 3** Fig. 6.16c-f, r-z, Fig. 6.17a, b.

Kol (1968b) Tafel VIII Fig. 32-33.

Distribution. SN. (DE, MC.)

Vegetative features. Cells cylindrical with rounded ends, 13-16 μm long by 4-7 μm wide. Chloroplast parietal, broadly lobed, 2-4 per cell (Fig. 6.16r-v). Papilla broad, slightly offset from apex.

Reproductive features. Zoospores 10-16 μm long by 3-5 μm wide. Spores grow to adult size before release and are aligned approximately parallel within sporangium (Fig. 6.16e, w). Resting cyst, 25-40 μm long, 8-12 μm wide, with 5-8 linear to slightly spiralled longitudinal flanges on cell wall (Fig. 6.16f, x-z, 6.17a, b).

Remarks. Vegetative cells of this species of *Chloromonas* differ significantly from others described by Ettl (1970) and in the literature on snow algae. The resting cyst with which it is apparently associated is most similar to *Scotiella nivalis* (Shuttleworth) Fritsch var. *californica* Kol as shown by Kol (1968b). *Scotiella* Fristch is no longer an accepted genus within the snow algae and *S. nivalis* var. *californica* Kol is almost certainly a resting cyst of a *Chloromonas*. However, although the size and number of flanges on the cell wall are approximately the same as those on the Mt Philistine specimen, they appear more spiralled and regularly arranged. Thus it is likely that this is a new species of *Chloromonas*.

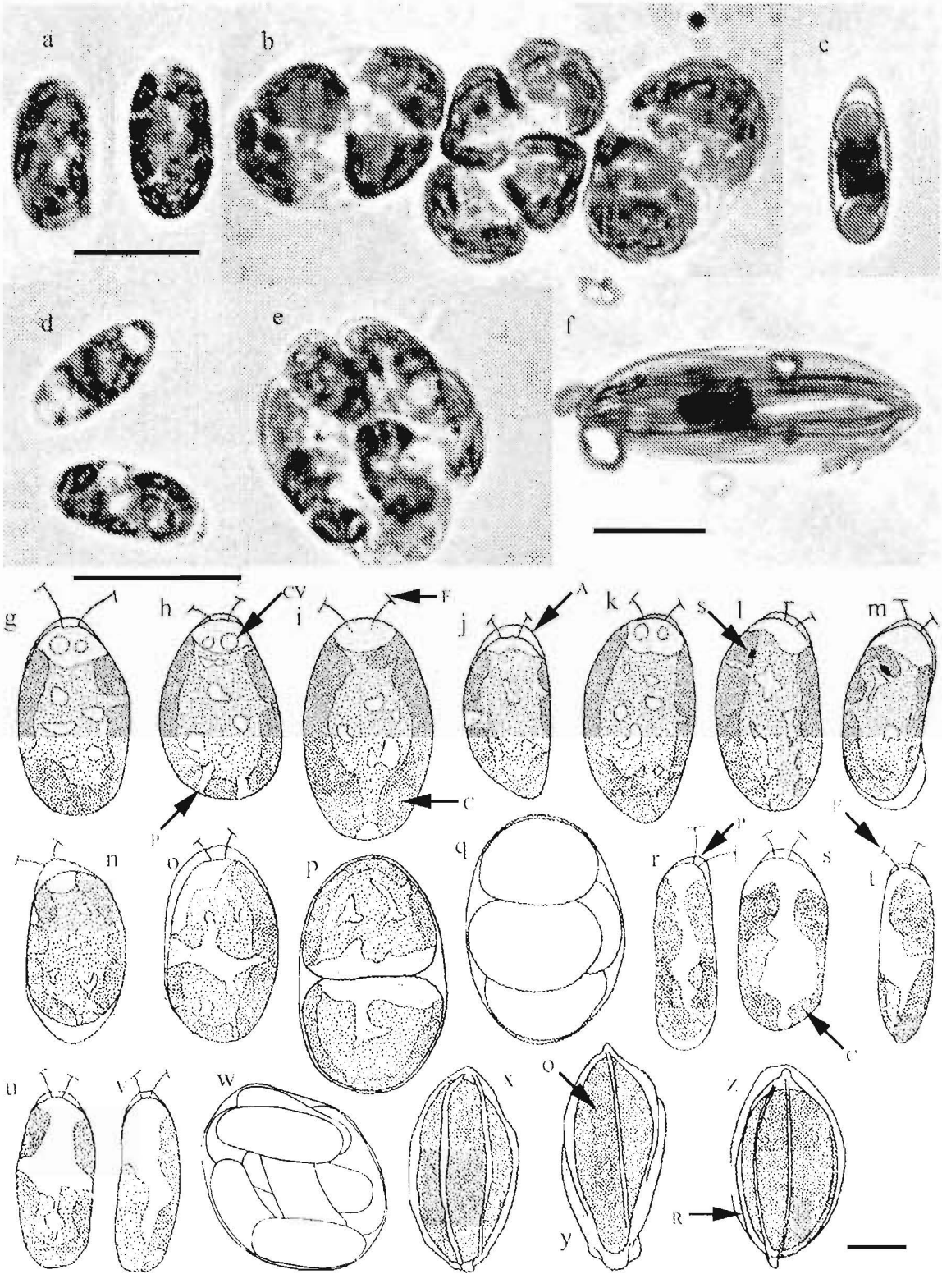


Fig. 6.16. a, b, g-q, *Chloromonas* sp. 2, liquid culture material: a, vegetative cells; b, zoosporangia; g-n, motile vegetative cells (F=flagella, shown truncated, CV=contractile vacuoles, C=chloroplast, P=perforations in chloroplast, A=swollen apical dome, S=stigma); o-q, process of zoospore formation culminating in 4-cell sporangium.

c-f, r-z, *Chloromonas* sp. 3, field material: c, preserved vegetative cell (note large oil droplets); f, resting cyst strongly resembling *Scotiella nivalis* var. *californica*. Liquid culture material: d, vegetative cells; e, zoosporangium (note difference in daughter cell alignment compared to b); r-v, motile vegetative cells (P=papilla, C=chloroplast, F=flagella); w, zoosporangium; x-z, resting cysts (O=orange cell interior, R=ribs on outer envelope, some spiralled).

All scales=10 µm (use scale in a for a-e, g for g-w, z for x-z).

Three cell types are included in the description of this taxon: cultured material, preserved field flagellates, and the resting cyst. Linking of these three cells is somewhat tenuous. Because field flagellates rupture on preservation (Fig. 6.16c), no interior features can be used to assess its identity. It is thought to be the same organism as the cultured specimens because it has the same dimensions and an identical papilla (compare Fig. 6.16c with Fig. 6.16d and with Fig. 6.16r), and was present initially in the samples from which the cultured cells appeared. The resting cyst is linked to vegetative cells because a sample from near Barker Hut, further south in the National Park, contained high numbers of both cell types. The issue could be resolved by generating the cyst in culture (it may be a zygospore).

***Chloromonas* sp 4** Fig. 6.17c-l.

Syn: *Scotiella antarctica* Fritsch

Kol (1968b) p137, Fig. VI: 1-9.

Distribution. SN (DE)

Features. Cells ellipsoidal, contents obscured by orange carotenoid pigment (Fig. 6.17c-f). Longitudinal flanges on cell wall, 6 per cell, linear (Fig. 6.17g) to slightly undulating (Fig. 6.17l). Attenuated apices formed by merger of 2 opposite or near-opposite flanges (Fig. 6.17g, i); the remaining 4 flanges merge into the apex at a slightly sub-polar position. Cells 25-30 μm long, 14-17 μm wide (32-34 μm x 20-23 μm with flanges).

Remarks. This is almost certainly a resting cyst of a *Chloromonas* snow alga, as shown by Hoham (1975), Hoham and Mullet (1977), and Hoham *et al.* (1979, 1983) for other species of *Scotiella* (see Chapter 1: Introduction). Fritsch (1912) commented on this possibility in the original description. Vegetative morphology is still unknown however. *S. antarctica* has been reported from Maritime Antarctica, Spitzbergen, the Caucasus and Balkan Mountains, and Alaska (Kol 1968b). It has not been found previously in New Zealand.

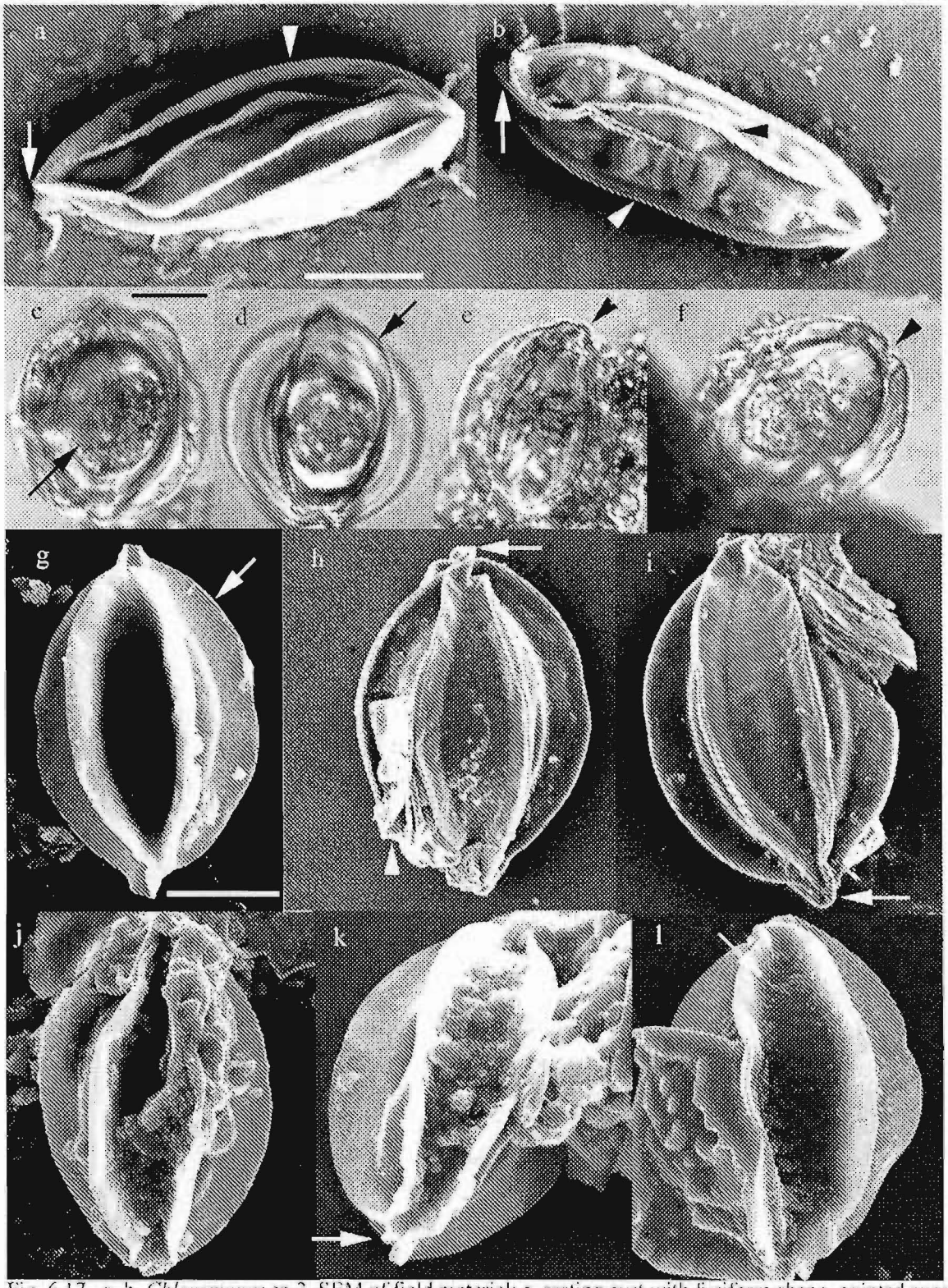


Fig. 6.17. a, b, *Chloromonas* sp.3, SEM of field material: a, resting cyst with fusiform shape, pointed apex (arrow) and spiralled outer flanges (arrowhead); b, fusiform end structure (arrow), spiralled flange (black arrowhead), and straight flanges (white arrowhead).

c-l , *Chloromonas* sp.4, identical to "*Scotiella antarctica*", Nomarski DIC of field matieral: c, living cell with orange contents (arrow); d, rare cell lacking adherent detritus, showing large straight flanges (arrow); e, cell embedded in mineral material (arrowhead indicates attenuated end structure); f, cell showing more rounded end structure (arrowhead). SEM: g, cell with little adherent detritus, showing large straight flanges (arrow); h, cell showing "dominant" flange on end structure (arrow), identical arrangement to the illustration of Kol (1968); i, same arrangement in more attenuated end structure (arrow), note that different flanges are "dominant" at each end; j, cell embedded in organic material; k, variation in end structure (arrow); l, cell with fine particulate detritus (arrow) covering surface.

All scales=10 µm (use scale in a for a-b, c for c-f, g for g-l).

Order Tetrasporales

Family Palmellopsidaceae

***Chlamydocapsa* sp.** Fig. 6.18a, b, g-l.

Ettl and Gärtner (1995) p297-298, Fig. 75d.

Distribution. Difficult due to confusion in field samples with *Gloeocystis papuana* (Watanabe) Ettl and Gärtner. Samples containing either of these genera from: MF, P, SO, LM (DE, EC, MC)

Vegetative features. Cells grouped irregularly in homogeneous mucilage (Fig. 6.18b, g); broadly ellipsoidal to pyriform, 11-14 μm long, 9-12 μm wide. Chloroplast parietal, cup-shaped, with numerous small lobes and incisions (Fig. 6.18g). Pyrenoid single. Contractile vacuoles not observed.

Reproductive features. Autospores ellipsoidal, 6-8 μm long, 5-6 μm wide, 4-8 in sporangia (Fig. 6.18i-k). Zoospores ellipsoidal, 7-8 μm long, 4-5 μm wide, with apical papilla, lacking stigma and pyrenoid (Fig. 6.18l).

Remarks. Homogeneous mucilage and lack of pyrenoid and stigma in zoospores contradict the generic assignment. However the only alternative, *Palmellopsis*, has a large unlobed chloroplast and colonies which are either macroscopic or of only 2-8 cells in size. Thus the alga can be placed with reasonable confidence in the genus *Chlamydocapsa*, especially since Ettl and Gärtner (1995) state that "mucilage is seldom without structure".

Cell and chloroplast shape are similar to those of the unidentified species of *Chlamydocapsa* described from Antarctica by Broady (see Ettl and Gärtner 1995), the zoospore of which also has a papilla.

Order Chlorococcales

Family Chlorococcaceae

***Chlorococcum tatrense* Archibald** Fig. 6.8d, h-k.

Ettl and Gärtner (1995) p315-316, Fig. 82a.

Distribution. P, MF, L, SO, LM, LV (MC)

Vegetative features. Young cells ellipsoidal (Fig. 6.8h), adult cells spherical (Fig. 6.8i), 13-23 μm diameter. Chloroplast parietal, cup-shaped, with numerous small lobes and small incisions, sometimes with perforations in older cells. Pyrenoid single (rarely two), with perforated starch sheath.

Reproductive features: Autospores (Fig. 6.8k) 7-11 μm long, 5-8 μm wide, 8-16(-32) per sporangium. Zoospores (Fig. 6.8j) ellipsoidal-cylindrical, approximately 7 μm long, 4 μm wide, with double papilla, 8 per sporangium.

Remarks. The complex multi-lobed single chloroplast, complete perforated starch sheath around the pyrenoid, spherical adult cells, small stigma and double papilla of the zoospore, and zoospore shape conform to *C. tatrense*. However, no contractile vacuoles have been observed.

C. tatrense has been isolated from snow detritus in Europe (Ettl and Gärtner 1995).

Class Chlorophyceae

Order Chlorellales

Family Myrmeciaceae

***Myrmecia* cf. *irregularis* (Petersen) Ettl & Gärtner** Fig. 6.18c-e, m-r.

Ettl and Gärtner (1995) p377-378, Fig. 105c.

Distribution. P, SO, MF, R, LV, LM (MC)

Vegetative features. Cells single, spherical to slightly pyriform. Adult cells 14-21 μm diameter. Chloroplast single, parietal, with 2-3 lobes and 2-3 deep incisions (Fig. 6.18m). Pyrenoid absent. Cell wall smooth, up to 2 μm thick (Fig. 6.18n).

Reproductive features. Autospores spherical, 4-10 μm diameter, up to 32 per sporangium. Sporangium round to slightly pyriform (Fig. 6.18p). Release occurs probably by dissolution of sporangium wall, but developing spores remain in clusters (Fig. 6.18d, e). Zoospores (Fig. 6.18r) naked, approximately 4 μm long, 2 μm wide, with stigma in parietal cup-shaped chloroplast, becoming spherical on cessation of motility. Position of chloroplast and stigma variable.

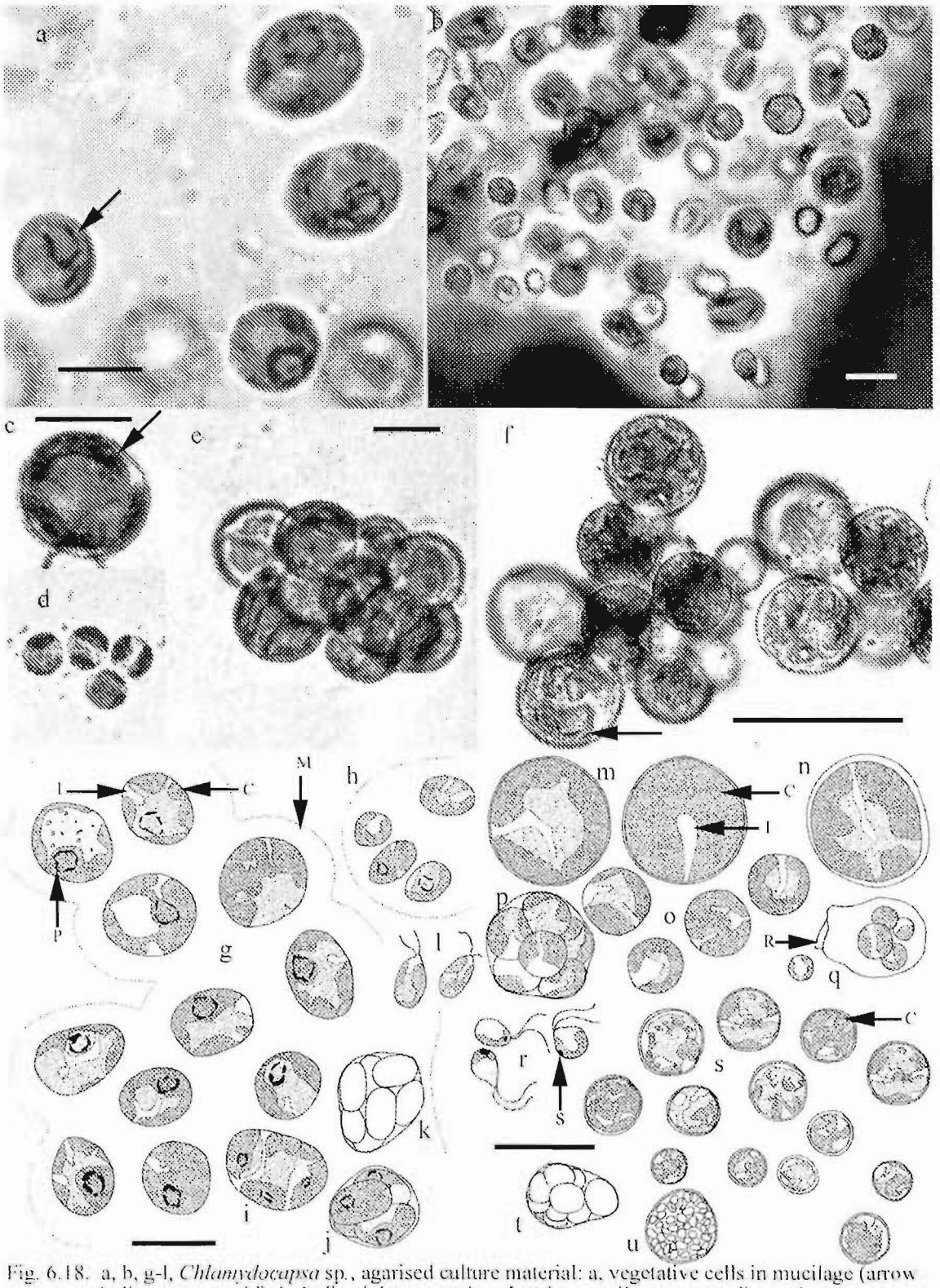


Fig. 6.18. a, b, g-l, *Chlamydocapsa* sp., agarised culture material: a, vegetative cells in mucilage (arrow indicates pyrenoid); b, Indian ink preparation showing mucilage surrounding colony; g, vegetative cells (P=pyrenoid, C=chloroplast, I=incision in chloroplast, M=mucilage); h, young cells; i, dividing cell; j-k, autosporangia; l, zoospores.

c-e, m-r, *Myrmecia* cf. *irregularis*, agarised culture material: c, mature vegetative cell (arrow indicates lobed chloroplast); d, newly released autospores; e, group of mature cells; m, mature cells, optical section and surface views of chloroplast left and right respectively (C=chloroplast, I=incision); n, mature cell with thicker cell wall and slightly pyriform shape; o, young cells; p, autosporangium; q, germination of sporangium by rupture (R) in wall; r, zoospores (S=stigma).

f, s-u, *Myrmecia* cf. *biatorellae*, agarised culture material: f, vegetative cells (arrow indicates one lobe of convoluted chloroplast); s, vegetative cells (C=chloroplast); t, autosporangium; u, possible zoosporangium.

All scales=10 μm (use scale in e for d-e, g for g-l, s for m-u).

Remarks. Chloroplast shape, cell shape and presence of zoospores suggest *M. irregularis*. However, smaller diameter range, within the limits of Ettl and Gärtner (1995), and variable position of the stigma in the zoospore are contradictory. The only alternative (*M. globosa* Printz) is ruled out by its wall thickenings and bell-shaped chloroplasts.

***Myrmecia* cf. *biatorellae* (Tschermak-Woess & Plessl) Petersen** Fig. 6.18f, s-u.
Ettl and Gärtner (1995) p375-378, Fig. 105b.
Distribution. R, LM, LV (EC, MC)

Vegetative features. Cells spherical, diameter 10-24 μm. Chloroplast parietal, convoluted and perforated (Fig. 6.18f, s), with numerous small lobes, especially in adult cells. Cell wall up to 3 μm thick.
Reproductive features. Autospores (Fig. 6.18t) 5-10 μm diameter, 2-4-8-16 per sporangium, varying sizes within sporangium. A structure thought to be a zoosporangium (Fig. 6.18u, containing 64 cells) was observed 2 days after flooding plate with fresh liquid medium, but spore release was not observed.
Remarks. Placing the alga in Myrmeciaceae assumes that the structure observed after flooding a culture was a zoosporangium. Size and occurrence of *M. biatorellae* according to Ettl and Gärtner (1995) are in agreement with those of the Mt Philistine specimen. However, shape variation in adult cells differs (especially as shown in their Fig. 105a). Their Fig. 105b shows cells containing a chloroplast with numerous small lobes, almost identical to that of the Mt Philistine alga. It is this that supports cautious assignment to *M. biatorellae*. However, this chloroplast morphology does not seem to be mentioned in the text, and is absent from their Fig. 105a. Also, only 4 autospores per sporangium have been reported for *M. biatorellae*.

M. biatorellae is reported from woodland soil and as a lichen photobiont, soil from Surtsey Island, and treebark in Japan (Ettl and Gärtner 1995).

cf. *Trochisciopsis tetraspora* Vinatzer Fig. 6.19a-c, h-m.

Ettl, and Gärtner (1995) p383-384, Fig. 108b.

Distribution. P, MF, SO, LM (EC)

Vegetative features. Cells spherical to slightly ellipsoidal, 7-13 µm wide. Cell wall thick, with 8-13 meridional ribs meeting at cell poles (Fig. 6.19c). Chloroplasts parietal, 1-3 per cell, with small incisions, in immature cells (Fig. 6.19k); up to 9 per cell in mature cells (Fig. 6.19h).

Reproductive features. None observed. Contents of many mature cells indistinct and may contain daughter cells.

Remarks: Spherical cell shape and distinctive cell wall with meridional ribs suggests *Trochisciopsis*. Number of ribs on the cell wall and incised chloroplasts in the young cells are most similar to *T. tetraspora*. However the cells are considerably smaller than the reported size range (diameter 20-40 µm) and no reproductive features were observed, despite large numbers of ribbed cells in the enrichment culture. It is therefore unknown what part of the life-cycle the ribbed cell represents. According to Ettl and Gärtner (1995) numerous zoospores, which subsequently form the ribbed cell, should be produced in four sporangia within the ribbed mother cell wall. The thinner appearance of the ribs in SEM (Fig. 6.19c) compared to LM (Fig. 6.19h) may be due to collapse of vacant space within the rib structure during preparation of samples for SEM. Immature chloroplasts resemble those of *Myrmecia*, which was also present in the same enrichment culture; however there is no direct evidence that the smooth-walled cells are a different form of the same organism.

T. tetraspora is reported from calcium-rich soils in the Italian Alps at 2000 m (Ettl and Gärtner 1995).

Family Chlorellaceae

***Chlorella* cf. *homosphaera* Skuja** Fig. 6.20d, s-ab.

Ettl and Gärtner (1995) p409, Fig. 119b p410.

Distribution. P, MF, R, LM, LV, SO (DE, MC)

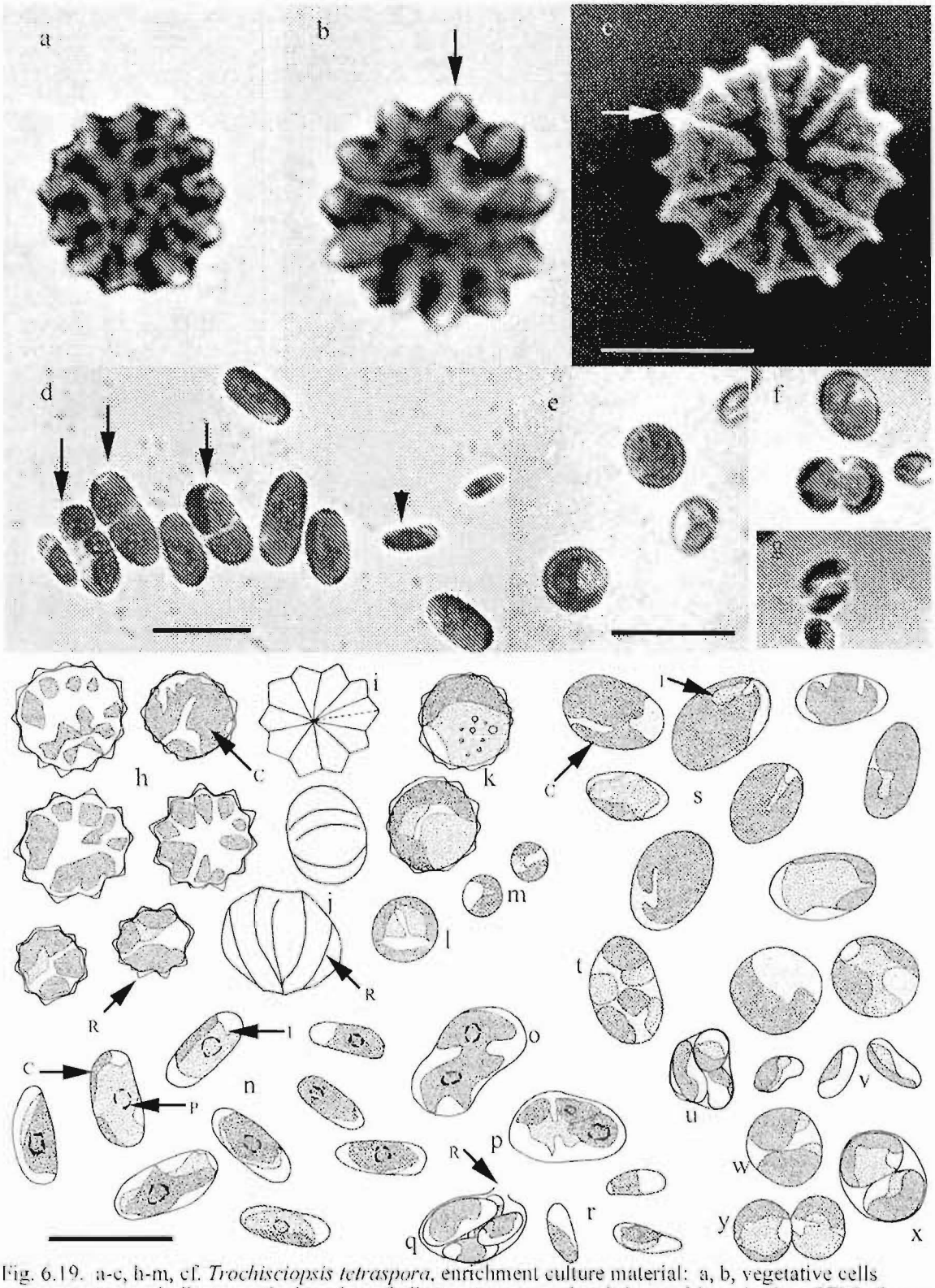


Fig. 6.19. a-c, h-m, cf. *Trochisciopsis tetraspora*, enrichment culture material: a, b, vegetative cells (arrow indicates optical section of rib structure, arrowhead shows chloroplast); c, SEM of vegetative cell showing rib pattern (arrow indicates rib); h, vegetative cells (C=chloroplast, R=rib); i, approximate rib structure as seen under LM (dotted line represents rib position); j, rare side view of cells (R=rib); k, less mature cells with reduced rib size; l, m, non-ribbed cells seen in same enrichment culture, may be *Chlorella* or *Myrmecia*.

d, n-r, cf. *Pseudochlorella*, agarised culture material: d, mature vegetative cells, autosporangia (arrows), newly released autospores (arrowhead); n, mature cells (C=chloroplast, P=pyrenoid, I=incision); o, p, dividing cells; q, autosporangium with rupturing wall (R); r, newly released autospores.

e-g, s-y, *Elliptochloris* cf. *reniformis*, agarised culture material: e, mature vegetative cells; f, formation of large autospores; g, formation of small autospores; s, mature cells (C=chloroplast, I=incision); t-v, formation of small autospores; w-y, formation of large autospores.

All scales 10 µm (use scale in c for a-c, e for e-g, n for h-y).

Vegetative features. Cells spherical to slightly pyriform, 6-13 μm diameter. Young cells spherical to ellipsoidal (Fig. 6.20s, y). Chloroplast parietal, bilobed, with two shallow to deep incisions (Fig. 6.20w). Pyrenoid absent. Cell wall thin and smooth. Large opaque granules present in cytoplasm of field specimens (as in Fig. 6.20d), diminishing with increasing subculturing.

Reproductive features. Autospores (Fig. 6.20aa-ab), 4-7 μm diameter, 2-4 per sporangium.

Remarks. Shape of chloroplast and absence of a pyrenoid support assignment to *C. homosphaera*. However Ettl and Gärtner (1995) record this species with a smaller size range (5.7-7.0 μm, although sporangia may be up to 11 μm), with some cells broadly ellipsoidal in shape, rather than slightly pyriform as observed in the adult cells of the Mt Philistine strain. Autospores are also larger than those reported for *C. homosphaera*. The adult vegetative state more closely resembles *Myrmecia astigmatica*, but absence of zoosporulation precludes its assignment to the Myrmeciaceae.

Ch. homosphaera has been found in aerophytic and soil habitats and growing on treebark (Ettl and Gärtner 1995). It is not included in New Zealand species lists (Cassie 1984).

***Chlorella* cf. *minutissima* Fott & Nováková** Fig. 6.20a-c, h-r.

Ettl and Gärtner (1995) p 409, p410 Fig. 119a.

Distribution. P, MF, R, LM, HM (MC)

Vegetative features. Adult cells (Fig. 6.20a) spherical, 3.5-5.5 μm in diameter. Young cells (Fig. 6.20r) ellipsoidal, 2.5-3.5 μm long, 1.5-2.0 μm wide. Chloroplast cup-shaped (rarely band-shaped), usually bilobed with two deep incisions. Pyrenoid absent. Adult cells may contain small granules in the cytoplasm (Fig. 6.20j).

Reproductive features. Autospores (Fig. 6.20b, c, r), 2-4-8 per sporangium.

Remarks. Small size of the cells, chloroplast shape, absence of a pyrenoid and number of autospores produced suggest *Chlorella minutissima*. Size range is slightly above that reported (2.0-3.5 μm diameter) by Ettl and Gärtner (1995).

C. minutissima has previously been found in soil from Surtsey Island and Argentina (Ettl and Gärtner 1995).

***Elliptochloris reniformis* (Watanabe) Ettl & Gärtner** Fig. 6.19e-g, s-y.

Ettl and Gärtner (1995) p424, Fig. 127d-f.

Distribution. SO, MF, PL, LM, LV (MC)

Vegetative features. Cells broadly ellipsoidal to spherical (Fig. 6.19e, s), 7-13 µm long, 4-8 µm wide. Chloroplast parietal, cup-shaped, usually with 2 or more deep incisions (Fig. 6.19s). Pyrenoid absent. Cell wall thin and smooth.

Reproductive features. Autospores in two forms: large form (Fig. 6.19f, w-y) ellipsoidal to spherical, 5-8 µm diameter, 2-4 per sporangium; small form (Fig. 6.19g, t-v) ellipsoidal, may be slightly curved, 4-6 µm long, 2-3 µm wide, 4-8-16 per sporangium.

Remarks. Two types of autospores and both spherical and elliptical mature cells are characteristic of *Elliptochloris*. It is possible that the smaller autospores represent only further stages of division of the larger ones, although the slightly curved shape of the smaller ones suggest that they may be distinct. Although the chloroplasts most typically have only two incisions and are thus bilobed, which is more characteristic of *E. bilobata* Tschermak-Woess, the curved small autospores place the alga in the species *E. reniformis* (Ettl and Gartner 1995).

E. reniformis has been reported from high mountain soils in Austria, and from soils in Papua New Guinea and Japan (Ettl and Gartner 1995).

***Muriellopsis* cf. *sphaerica* Broady** Fig. 6.20e, ac-al.

Ettl and Gärtner (1995) p417, 420, Fig. 123c.

Distribution. P, SO, MF, LV (MC)

Vegetative features. Cells single, 6-10 µm long by 6-8 µm wide; mature cells (Fig. 6.20ac-ag) spherical (rarely ellipsoidal); young cells (Fig. 6.20ak-al) spherical to ellipsoidal. Chloroplasts parietal, 1-4 per cell, one of which contains a pyrenoid with complete starch sheath (Fig. 6.20ac).

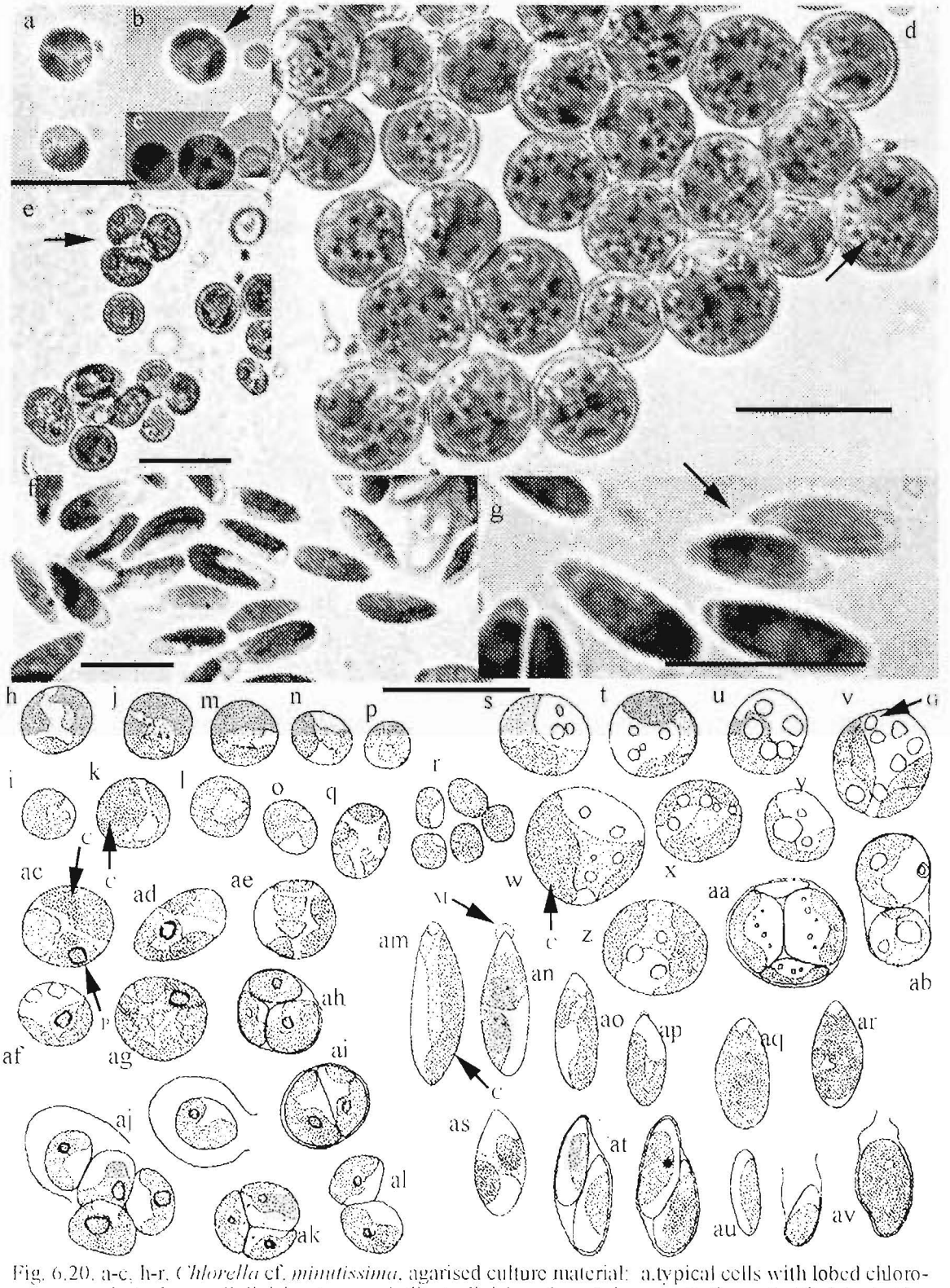


Fig. 6.20. a-c, h-r, *Chlorella* cf. *minutissima*, agarised culture material: a,typical cells with lobed chloroplasts; b, c, cell division (arrows indicate division planes); h-p, vegetative cells (C=lobed chloroplast); q, dividing cell (chloroplast division visible); r, newly released daughter cells.

d, s-ab, *Chlorella* cf. *homosphaera*, agarised culture material: d, vegetative cells (arrow indicates granular material in cytoplasm); s-z, vegetative cells (C=lobed chloroplast, G=granules, note larger size of granules in u, v, y from an earlier subculture); aa, ab autopsorangia.

e, ac-al, *Muriellopsis* cf. *sphaerica*, agarised culture material: e, group of cells (arrow indicates cell tetrad released from sporangium); ac-ag, vegetative cells (P=pyrenoid, C=chloroplasts, note variation in shape); ah-ai, autosporangia; aj, spore release; ak-al, newly released adhering cells.

f, g, am-av, *Pseudococcomyxa simplex*, agarised culture material: f, vegetative cells; g, autosporangium (arrow) with oblique division plane; am-as, vegetative cells (C=chloroplast, M=mucilage); at, autosporangia; au-av, newly released cells.

All scales=10 μm (use scale in a for a-c, use scale in s for h-av).

Reproductive features. Autospores (Fig. 6.20e, ah-aj) spherical to ellipsoidal, 4-6 µm long by 3-5 µm wide; 2-4 per sporangium. Spores characteristically released as a tetrad from the sporangium (Fig. 6.20e), which may remain intact until cells are adult size.

Remarks. Complete starch sheath surrounding the pyrenoid most resembles *M. sphaerica*. It is slightly smaller than the 13 µm minimum diameter reported by Ettl and Gärtner (1995) for *M. sphaerica*, although it is closer in size to this species than to others. Autospore size is in agreement with *M. sphaerica* but autospore shape (spherical in *M. sphaerica*) differs in the Mt Philistine specimens.

M. sphaerica has been reported from the Vestfold Hills, Antarctica, in damp soils and the excreta and moult from elephant seals. It is not included in New Zealand species lists (Cassie 1984).

cf. *Pseudochlorella* sp. Fig. 6.19d, n-r.

Ettl and Gärtner (1995) p421.

Distribution. MF, LV (MC)

Vegetative features. Cells narrowly ellipsoidal to slightly pyriform, 8-12 µm long, 3-6 µm wide. Chloroplast parietal, along one side of cell, sometimes slightly lobed, containing one central pyrenoid surrounded by large starch grains (Fig. 6.19n).

Reproductive features. Autospores (Fig. 6.19o-r) 6-7 µm long, 2-4 µm wide, 2-4-8 per sporangium.

Remarks. Pseudochlorella as described by Ettl and Gärtner (1995) is confusing. It is distinguished by packet-like groups of cells and having an axial chloroplast; however, illustrations of *P. pyrenoidosa* (Fig. 125a, p420) clearly show a parietal chloroplast. The text is ambiguous on this point. Ellipsoidal shape in the adult stage of the Mt Philistine organism and one type of autospore (distinct from *Elliptochloris*) suggest *Pseudochlorella.*

Pseudochlorella pyrenoidosa has been found as a lichen photobiont and in alpine soils in Italy (Ettl and Gärtner 1995).

***Pseudococcomyxa simplex* (Mainx) Fott** Fig. 6.20f, g, am-av.

Ettl and Gärtner (1995) p425-426, Fig 127h. Broady (1987a) p26-27, Fig. 1, 5-7.

Distribution. MF, P, SO, R, LM, LV, ASN

Vegetative features. Cells single, pyriform. Adult cells 9-14 µm long, 3-5 µm wide. Chloroplast parietal, cup-shaped, usually aligned on one side of cell (Fig. 6.20am), often with lobes or incisions in older cells (Fig. 6.20ao); single, except in older cells in which it may split into two of usually opposite orientation (Fig. 6.20an, as). Pyrenoid absent. Cell wall thin and smooth. Mucilage cap develops on pointed apex of adult cells (Fig. 6.20an).

Reproductive features. Autospores 6-8 µm long, 2-3 µm wide, 2 per sporangium, formed by oblique division (Fig. 6.20g, at). Sporangium pyriform. Release occurs by split in apex of sporangium wall. Cell closest to split is released, while the other may be retained in remains of sporangium (Fig. 6.20av). Remnants of sporangium wall may be seen on large adult cells.

Remarks. Ettl and Gärtner (1995) reported 2-4 autospores per sporangium, whereas only 2 have been observed in the present strain, and did not note the retention of the sporangium wall by one of the released autospores, which is characteristic of the Mt Philistine strain. This feature was reported by Broady (1987a), although he also noted 2-4-8 autospores per sporangium. Size range, and shapes of cells and chloroplasts agree well with these published descriptions.

Pseudococcomyxa simplex has been reported from soils in Europe, the surface of Antarctic glaciers, and unspecified algal crusts in Japan (Ettl and Gärtner 1995). Broady (1987a) reported its presence in grassland soils in Australia and as an epiphyte on mosses, in lithosols, in volcanic fumarolic soils and as a chasmoendolithophyte in Antarctica. It is not included in New Zealand species lists (Cassie 1984).

***Scotiellopsis terrestris* (Reisigl) Punčochářová & Kálina** Fig. 6.21a-d, f-p.

Punčochářová and Kalina (1981) p136-143, Fig. 15c-d, 16, 17, 19.

Distribution. SO, MF, R, LM, LV (EC, MC)

Vegetative features. Cells single, fusiform and citriform, with pronounced polar thickenings (Fig. 6.21f), located on or slightly deviated from longitudinal axis of cell.

Adult cells 14-20 µm long, 8-11 µm wide. Cell wall has 8-12 distinct meridional ribs (Fig. 6.21c, d), clearly visible in LM (Fig. 6.21b). Chloroplasts parietal, discoidal, 2-7 per cell. Pyrenoid single (Fig. 6.21a). Old cells develop large vacuoles or oil globules which obscure chloroplast shape (Fig. 6.21m).

Reproductive features. Autospores (2-4-8 per sporangium), 8-16 µm long, 5-8 µm wide. Spore release occurs through a split in sporangium wall which develops from cell apex (Fig. 6.21m-o). Adult cells may be retained temporarily in remains of sporangium wall (Fig. 6.21p).

Remarks. Cell size and shape and number of ribs on cell wall are in close agreement with *S. terrestris* (Punčochářová and Kalina 1981). In contrast, the nuclei of the Mt Philistine specimens are not easily visible. Punčochářová and Kalina (1981) also report that some strains of *S. terrestris* form giant spherical spores, but they did not view these as being of major taxonomic importance. These have not been observed in the Mount Philistine strain.

Description of the chloroplast of *S. terrestris* by Punčochářová and Kalina (1981) is confusing because it is drawn and described as being in several parts, or as more than one chloroplast (p138) but elsewhere noted that it may break up from a single structure during cell aging (p143). However, the critical features for identification of the species are cell size and shape, and number and prominence of ribs on the cell wall. These features are all in agreement.

S. terrestris is reported from mountain and high mountain conditions, in the superficial soil layer, on wet ground, and occasionally in snow (Punčochářová and Kalina 1981). Its presence in snow is intriguing because of its similarity to resting cysts of some *Chloromonas* snow algae, and the consequent implications for identification of field specimens from snow samples. It has not been included in New Zealand species lists (Cassie 1984).

Family Radiococcaceae

***Coccomyxa gloeobotrydiformis* var. A** Fig. 6.22a, b, h-t.

Ettl and Gärtner (1995) p445-447, Fig. 135c.

Distribution. P, R, SO, LM, LV (DE, EC, MC)

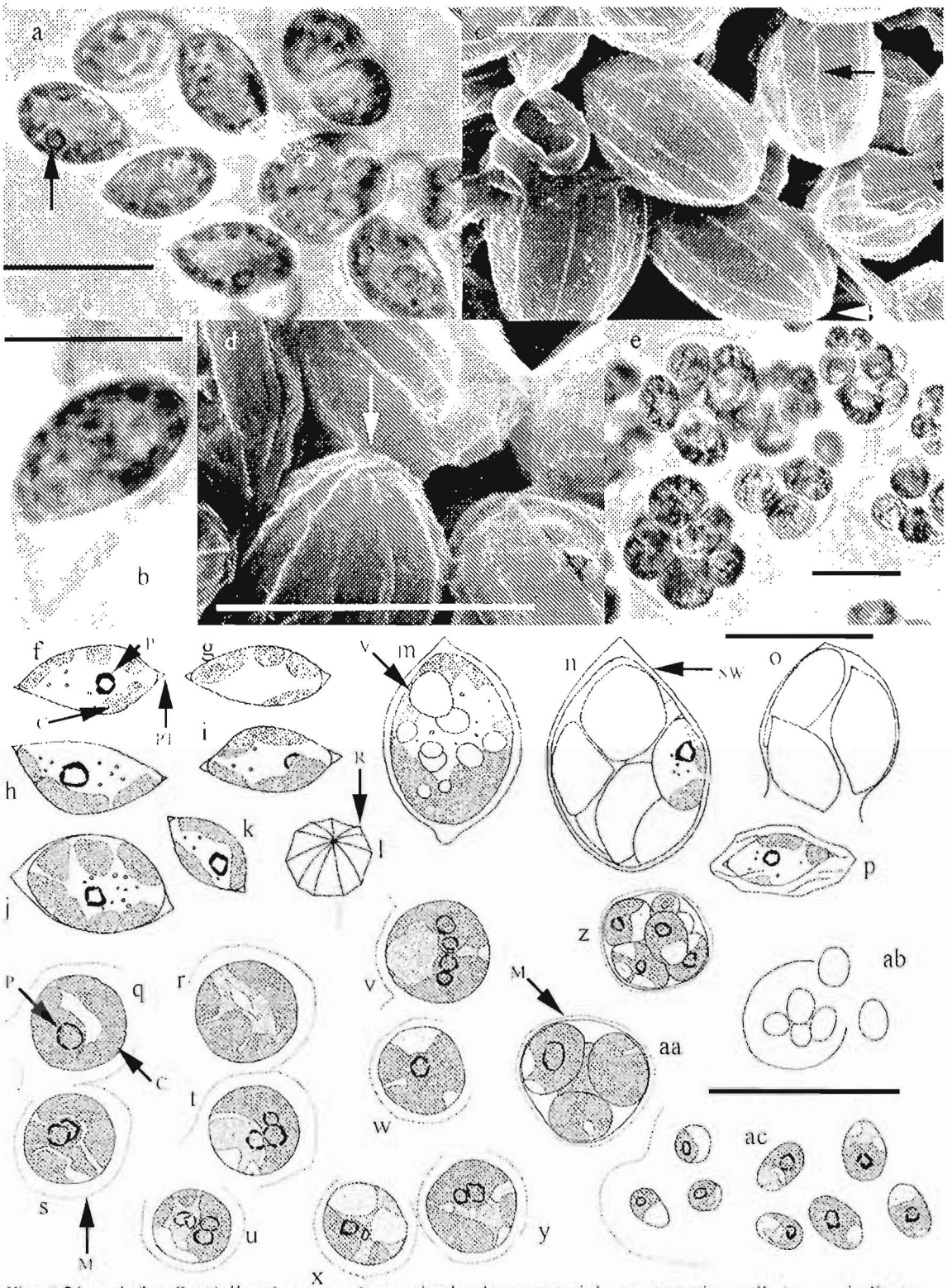


Fig. 6.21. a-d, f-p, *Scotiellopsis terrestris*, agarised culture material: a, vegetative cells (arrow indicates pyrenoid); b, cell in remains of sporangium wall; c, SEM of vegetative cells (arrow indicates longitudinal ribs on cell wall, arrowhead indicates rib fusion at cell apex; d, SEM of vegetative cells (arrow indicates rib pattern at cell posterior); f, vegetative cell in optical section (P=pyrenoid, PT=polar thickening, C=chloroplast); g, same cell in surface view; h, cell showing apices offset from longitudinal axis; i, cell with obscured pyrenoid; j, cell with pronounced apical wall thickenings; k, young cell; l, end view in LM showing ribs (R); m, old cell with large vacuoles (V); n, autosporangium (SW=thick sporangium wall); o, spore release; p, spore retained within wall.

e, q-ac, *Gloeocystis papuana*, agarised culture material: e, cells in colonial mucilage; q-y, vegetative cells with varying number of pyrenoids (P), chloroplast (C) shape and mucilage (M) thickness; z-aa, autosporangia (M=mucilage); ab, spore release; ac, young cells in mucilage.

All scales=10 µm (use scale in o for f-p, ac for q-ac).

Vegetative features. Cells irregularly distributed in colourless, homogeneous, diffluent mucilage (Fig. 6.22b). Cells spherical to ellipsoidal, 6-8 μm long by 4-6 μm wide. Chloroplast parietal (Fig. 6.22h-o), cup-shaped, may be bilobed, single (rarely 2). Pyrenoid absent. Cell wall smooth and thin.

Reproductive features. Autospores (Fig. 6.22a, p-t) 3-5 μm long, 2-4 μm wide; 2-4-8-16 per sporangium. Sporangium spherical to ellipsoidal, and surrounded by thicker mucilage than adult cells. Sporangium wall splits to release spores through small opening; empty sporangium always cup-shaped (Fig. 6.22s-t).

Remarks. No pyrenoid is present in this alga, distinguishing it from *Gloeocystis*. It is assigned to *C. gloeobotrydiformis* on the basis of ellipsoidal cell shape, thin mucilage, and cell size. However, mucilage surrounding the colony is thin around adult cells, and is not lamellate as shown by Ettl and Gärtner (1995).

The species has been reported from soils from the Himalayas and Antarctica (Ettl and Gärtner 1995). It has not been included in New Zealand species lists (Cassie 1984).

***Gloeocystis papuana* (Watanabe) Ettl & Gärtner** Fig. 6.21e, q-ac.

Ettl and Gärtner (1995) p444-445, Fig. 134c.

Distribution. Complicated by similarity to *Chlamydocapsa* when seen in field samples. Refer to *Chlamydocapsa* for distribution of cells belonging to either of these genera.

Vegetative features. Cells in large colonies surrounded by colourless homogeneous mucilage (Fig. 6.21e, s). Adult cells spherical, 11-17 μm wide; chloroplast parietal, cup-shaped, may have deep incisions and 2-4 lobes, with 1-4 pyrenoids surrounded by perforated starch sheaths (Fig. 6.21q-y).

Reproductive features. Autospores (Fig. 6.21z-aa) ellipsoidal, 6-9 μm long, 3-8 μm wide, 2-4-8 per sporangium. Mucilage thin around autosporangium (Fig. 6.21z), but thick around young cells (Fig. 6.21ac). In some strains the sporangium wall enlarges and is retained around groups of adult cells.

Remarks. Number and distribution of pyrenoids within the chloroplast assign the alga to *Gloeocystis*. Homogeneous mucilage contradicts this placement (Ettl and Gärtner 1995). However, the species *G. papuana* is described as lacking concentric mucilage layers. Cell size and number of pyrenoids also agree with the published account. There

is a strong possibility of confusion between this species and *Chlamydocapsa* from Mt Philistine when production of zoospores cannot be tested (e.g. when examining field samples).

G. papuana is reported from soils in Papua New Guinea (Ettl and Gärtner 1995). It has not been included in New Zealand species lists (Cassie 1984).

Family Oocystaceae

cf. *Oocystis minuta* Guillard, Bold & MacEntee Fig. 6.22c, d, u-ad.
Ettl and Gärtner (1995) p457-458, Fig. 140c.
Distribution. P, MF, R, LV, LM (MC)

Vegetative features: Cells single, ellipsoidal to pyriform. Adult cells 10-16 µm long, 5-9 µm wide. Chloroplast single, parietal, aligned on one side of cell (Fig. 6.22x). Pyrenoid single (Fig. 6.22w) or sometimes absent. Cell wall thin and smooth, except at cell poles where apical thickenings may develop at one end (Fig. 6.22z), rarely both ends (Fig. 6.22y).
Reproductive features. Autospores 5-9 µm long, 2-3 µm wide; 2-4-8 per sporangium. Sporangium commonly irregular to pyriform in shape, due to presence of one larger spore (Fig. 6.22ac). Release occurs by a split in apex of sporangium wall.
Remarks. Single pyrenoid, cell dimensions, chloroplast shape and apical thickening at one pole are characteristic of *Oocystis minuta.* However, the autosporangium containing one spore which is larger than the others is more characteristic of certain species of *Chlorella.* However, *Chlorella* does not form apical thickenings (Ettl and Gärtner 1995).

O. minuta has been found in soils from the USA, Japan, and Surtsey, and variations have been described from Japanese forest soils and Antarctic mineral fines (Ettl and Gärtner 1995). It has not been included in New Zealand species lists (Cassie 1984).

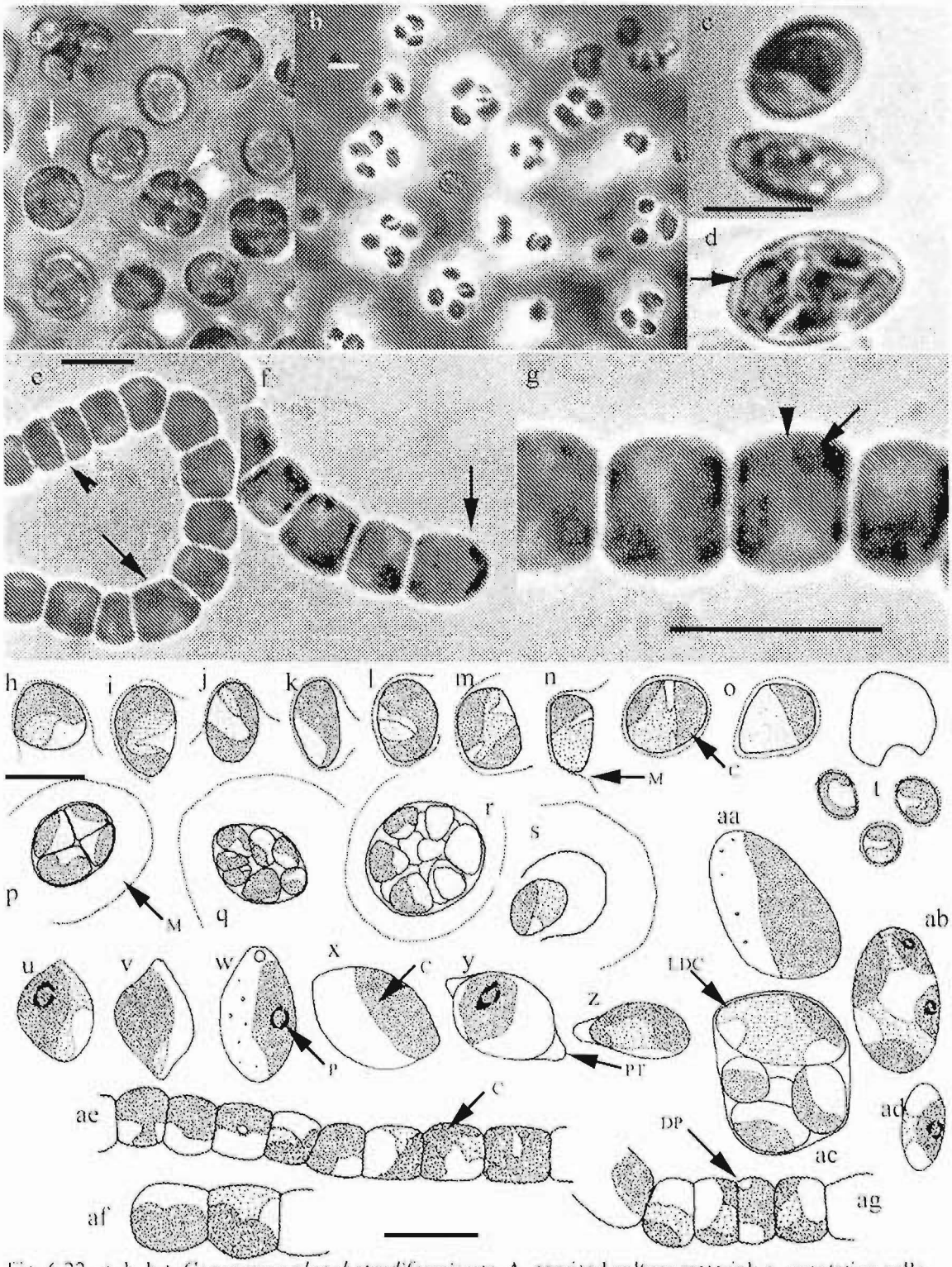


Fig. 6.22. a, b, h-t, *Coccomyxa gloeobotryediformis* var. A, agarised culture material: a, vegetative cells (arrow) and autosporangia (arrowhead); b, Indian ink preparation showing mucilage; h-n, vegetative cells in mucilage (M) with various cell and chloroplast shapes; o, cells released from colonies with thin mucilage (C=chloroplast); p-r, autosporangia (M=thick mucilage); s, release of single cell from sporangium; t, release of several daughter cells.

c, d, u-ad, cf. *Oocystis minuta*, agarsied culture material: c, vegetative cells; d, autosporangium with one larger daughter cell (arrow); u-x, typical vegetative cells (C=chloroplast, P=pyrenoid); y, cell with two polar thickenings (PT); z, cell with one polar thickening; aa, unusually large cell; ab, dividing cell with multiple pyrenoids; ae, autosporangium with one large daughter cell (LDC); ad, newly released spore.

e-g, ae-ag, *Coccothrix* cf. *chlorolobata*, agarised culture material: e, filament (arrowhead shows recent division, arrow shows impending division; f, filament showing broadly rounded terminal cell (arrow); g, detail of multilobed chloroplast(arrowhead to incision, arrow to lobe); ae, mature filament (C=chloroplast); af, rounded cell at terminus; ag, cell division (DP=division plane).

All scales=5 µm (use scale in c for c-d, e for e-f, q for i-ae, af for ae-ag).

Order Gloeotilales

Family Gloeotilaceae

***Coccothrix* cf. *chlorolobata* Broady & Lokhorst** Fig. 6.22e-g, ae-ag, Fig. 6.23.

Broady and Lokhorst (2000).

Distribution. MF, R (MC)

Vegetative features. Filaments short, up to approximately 30 cells, with pronounced constrictions at transverse walls. Cells doliiform, 3.0-5.0 µm long, 2.0-3.0 µm wide. Chloroplast parietal, usually against one side of cell, frequently bilobed (Fig. 6.22g, ae). Terminal cells broadly rounded (Fig. 6.22af.). Cell wall thin and smooth (Fig. 6.22f).

Reproductive features. Simple division of cells within filaments (Fig. 6.22f, ag). Filaments readily fragmented.

Remarks. The presence of two membranes surrounding the chloroplast and thylakoid stacks of 2-6 (Fig. 6.23c) confirm the placement of this alga in the Chlorophyta. It most resembles *Coccothrix chlorolobata* from Antarctica, which has been placed in the Gloeotilales following ultrastructural study (Broady and Lokhorst 2000). However, the Mt Philistine strain has slightly narrower cells than the Antarctic species, which may be up to 5.0 µm wide. It may be a new species of this recently-erected genus. Single cells resemble *Stichococcus chlorelloides* Grintzesco & Péterfi, but this does not form filaments, and has a smaller, non-lobed chloroplast (Ettl and Gärtner 1995).

Coccothrix chlorolobata was found in mineral soil from an ice-cored moraine. It has not previously been found in New Zealand.

Class Charophyceae

Order Klebsormidiales

Family Klebsormidiaceae

***Klebsormidium elegans* Lokhorst** Fig. 6.24d-f, j-m.

Lokhorst (1996) p 28-30, 113-117, Fig. 149-180.

Distribution. SO, P, MF, LM, LV, ASN (MC)

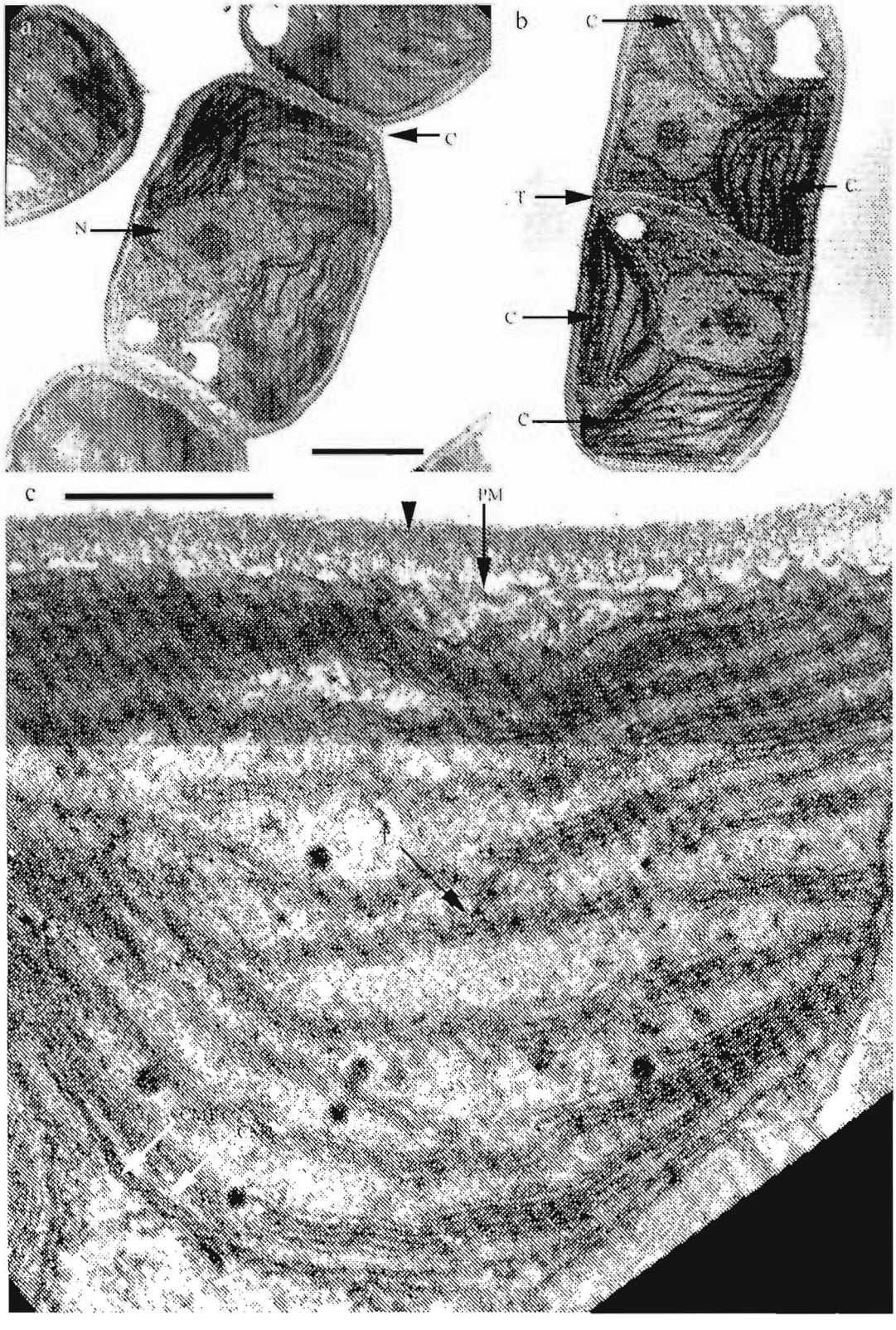


Fig. 6.23. *Coccothrix* cf. *chlorolobata*, TEM of agarised culture material: a, portion of filament with constrictions between cells (C) and nucleus (n) visible; b, dividing cell showing new transverse wall (T) and four chloroplasts (C), note radial symmetry of chloroplast arrangements in daughter cells; c, detail of portion of cell containing chloroplast, showing smooth cell wall (arrowhead), plasma membrane (PM), thylakoid stacks (T), and two membranes (CM1, CM2) surrounding chloroplast.

Scale bars: a =2 µm (use for a, b), c 0.5 µm.

Vegetative features. Filaments uniseriate, unbranched, straight to twisted or twined (Fig. 6.24m), 9.0-14.0 μm wide, indeterminate in length. Young cells cylindrical (Fig. 6.24d, e, j), becoming doliiform with age (Fig. 6.24k), 9-14 (-17) μm long, approximately isodiametric (length:width = (0.5-) 0.8-1.4). Chloroplast parietal, girdle-shaped, incompletely circling cell lumen. Pyrenoid single, with perforated starch sheath (Fig. 6.24k), not visible in all cells.

Reproductive features. Growth by vegetative division (Fig. 6.24e). Filament not easily fragmented when grown on agarised media; in liquid cultures H-shaped wall structures are formed between cells at points of fragmentation (Fig. 6.24f, l). Zoospores not observed.

Remarks. Cell size and shape, absence of mucilage or pseudobranches, a non-incised chloroplast and absence of zoospores assign this alga to *K. elegans*. Although a lobed chloroplast was not observed, only some of the illustrations of Lokhorst (1996) show this feature. It is possible that the alga actually belongs to the genus *Ulothrix* in the Ulvophyceae. However, the absence of a holdfast and the presence of H-shaped wall structures and ready fragmentation in liquid cultures suggests otherwise. To distinguish between these genera would require cytokinetic studies or observation of a zoospore. If it belongs in *Klebsormidium* then *K. elegans* is the most suitable species. Lokhorst (pers. com.) identified this isolate as *K. elegans*.

K. elegans has been reported from tree bark and is "sporadically distributed in Central and Western Europe" (Lokhorst 1996). New Zealand lists predate the erection of this species. It is possible that it has been recorded previously as a species of *Ulothrix* or *Klebsormidium*.

***Klebsormidium* cf. *flaccidum* (Kützing) Silva, Mattox & Blackwell** Fig. 6.24a-c, g-i. Lokhorst (1996) p 73-74, 91-96, Fig. 31-68.

Distribution. P, MF, SO, LM, LV (DE, EC, MC)

Vegetative features. Filaments uniseriate, unbranched, straight to curved, free-floating, 5.0-6.0 μm wide, often exceeding 150 cells in length. Cells cylindrical, 5-11 μm long, usually longer than wide (length:width = 0.8-2.2). Cell wall thin and smooth. Chloroplast parietal, girdle-shaped, incompletely circling cell lumen. Pyrenoid single, surrounded by large starch grains.

Reproductive features. Growth of filaments by simple division. Filaments readily fragment (especially when older) into 1 to ~15 cell lengths (Fig. 6.24b, c, h, i). Zoospores not observed, even after flooding agarised culture with liquid medium.

Remarks. The alga is assigned to *K. flaccidum* due to cell shape and dimensions, length attained by filaments, and ease of dissociation of filaments. However, no zoospores were observed (which are reported to be easily inducible) and only benthic "tufts" are apparent in liquid culture, the skeins reported to float on the surface (Lokhorst 1996) being absent. Species which are reported not to produce zoospores (Lokhorst 1996) all have cells which are too large, as do those species which develop only one growth form. Also the organism appears to grow slowly in liquid medium and it is possible that not enough time had elapsed for the development of two growth forms at the time of observation. Lohorst (pers. com.) identified this isolate as *K. flaccidum*.

K. flaccidum has been reported from rock surfaces, as epiphytes on plants, and as periphyton in Europe (Lokhorst 1996). In New Zealand it has been found (as *Chlorhormidium flaccidum*) in Taupo, Tekoa, and Omarama soils, Blackstone Hill soil (Cassie 1984) and on the surface of peat underlying *Poa astonii*, *Olearia lyalii*, and *P. tennantiana* vegetation on the Snares Islands (Flint and Fineran 1969).

***Raphidonema nivale* Lagerheim** Fig. 6.25c-g, aa-ac.

Hoham (1973).

Distribution: SN (DE, MC)

Vegetative features. Cells in liquid culture cylindrical with one tapered end and one rounded end or with two tapered ends (Fig. 6.25c, e, aa), 9-26 μm long by 2-3 μm wide. Cells in agarised culture medium cylindrical, 10-17 μm long by 2.5-3.5 μm wide, forming filaments of indefinite length with tapered apices on the terminal cells (Fig. 6.25d, ac). Tapers become increasingly rounded in older cultures (Fig. 6.25f, g, ab). Chloroplasts parietal, platelike (rarely bilobed), 1-2 per cell, symmetrical, pairs usually on same side of cell.

Reproductive features. Division begins by a constriction and subsequent division of the chloroplast. Cells divide symmetrically to give two identical daughter cells. The daughter cells in liquid culture may remain attached for some time before separation to

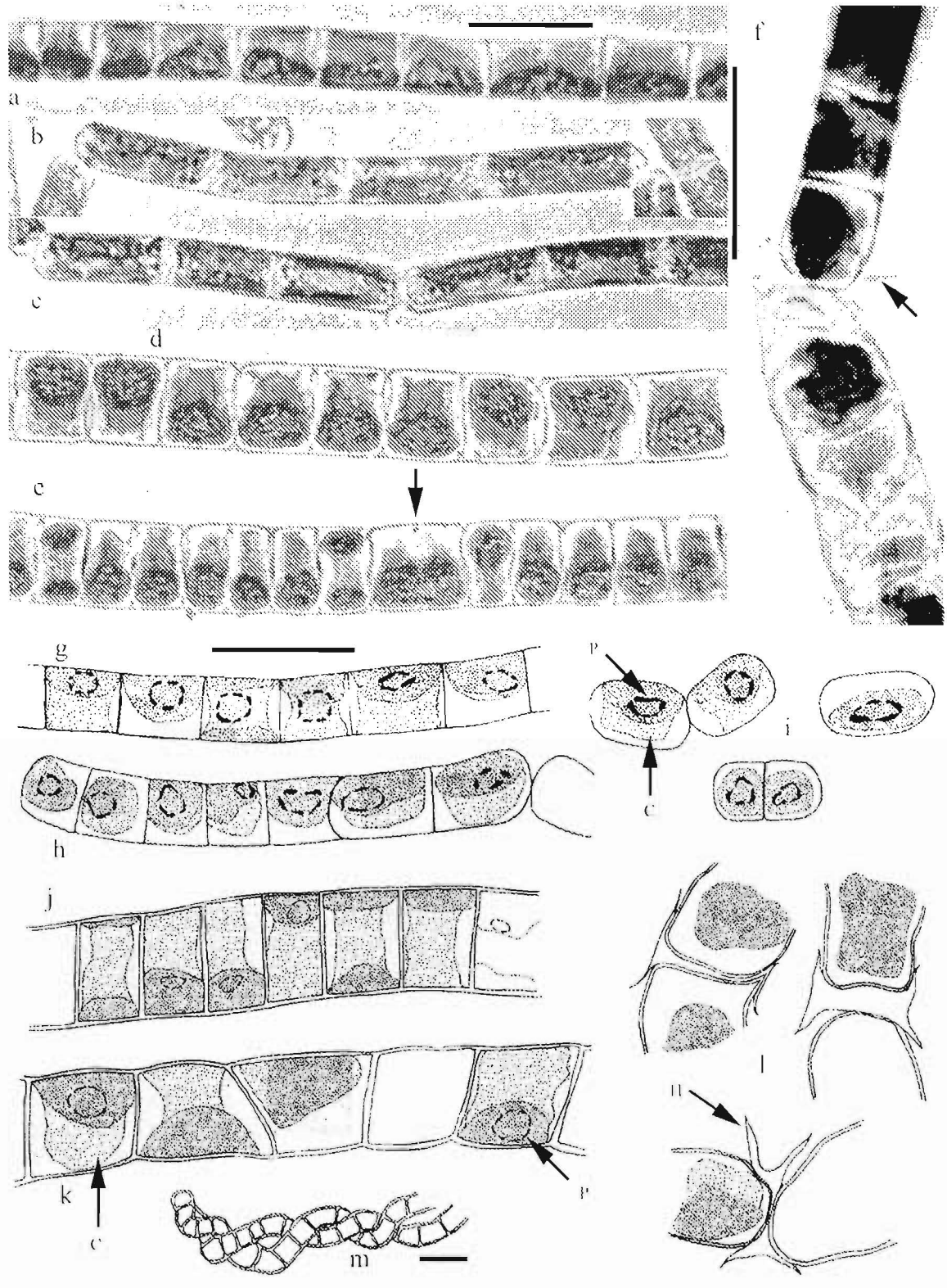


Fig. 6.24. a-e, g-i, *Klebsormidium* cf. *flaccidum*, agarised culture material: a-e, filaments from agarised culture displaying different cell length and ease of fragmentation; g, stable filament; h, fragmenting filament; i, single cells and cell pairs from fragmentation of filaments (P=pyrenoid, C=chloroplast).

d-f, j-m, *Klebsormidium elegans*, agarised culture material: d, typical filament; e, filament showing dividing cell (arrow indicates point of formation of new cell wall); f, filament showing H-shaped wall structure (arrow); j, young filament; k, old filament with doliiform cells (P=pyrenoid, C=chloroplast); l, filaments displaying H-shaped structures (H) of various forms; m, typical filament morphology in culture.

All scales=10 μm (use scale in a for a-e, g for g-l).

give two cells each with one rounded and one tapered end, which subsequently grow tapers from the rounded ends. Filaments readily fragmented.

Remarks. Pleiomorphism is notable in *Raphidonema* (Hoham 1973). Ability of cells to form filaments with tapered apices places the alga in this genus; however, at least in young liquid cultures, paired cells of *Koliella* form are observed. Hoham (1973) showed that culturing is required to accurately identify algae in the *Raphidonema/Koliella* complex, and that some forms of *R. nivale* strongly resemble cells previously assigned to the genus *Koliella*. It is possible that the genus *Koliella* is invalid in the snow microflora.

Wide size range of cells and their dominant shape is very similar to that reported by Hoham (1973), although a distinct nucleus and the more "bizarre" cell shapes and cells with a holdfast described by Hoham (1973) have not been observed. Older filaments with more rounded terminal cells are very similar to those found in Antarctica by Ohtani *et al.* (1998), and assigned to "*Raphidonema* sp".

Although this alga grew rapidly at 3°C in most cultures made from summer snow samples, very few cells were found during direct observation of snowmelt. *R. nivale* is capable of growth at temperatures up to at least 15°C (Hoham 1973), a much higher temperature than that endured by other snow algae on Mt Philistine. This implies that the alga may simply be a contaminant, dispersed onto snow by wind from other habitats. However, repeated examination and culturing from other habitats local to the snow sites have failed to detect the species anywhere except in snow.

R. nivale has been reported from snow in the US, Ecuador, Europe, Greenland, Spitzbergen, Japan, and Antarctica (Hoham 1973). Fukushima (1963) found the species growing in an Antarctic stream. It has not been included in New Zealand species lists (Cassie 1984), but the genus *Raphidonema* has previously been found in snow (Thomas and Broady 1997).

***Stichococcus* cf. *bacillaris* Nägeli** Fig. 6.25a, h-r.

Ettl and Gärtner (1995) p605-606, Fig. 204e.

Distribution. P, MF, R, LM, LV, ASN. (MC.)

Vegetative features. Cells straight cylindrical, rarely slightly curved (Fig. 6.25j, l, m), with rounded ends, 4-14μm long by 2-4μm broad. Cells 1.8-4.3 times longer than broad

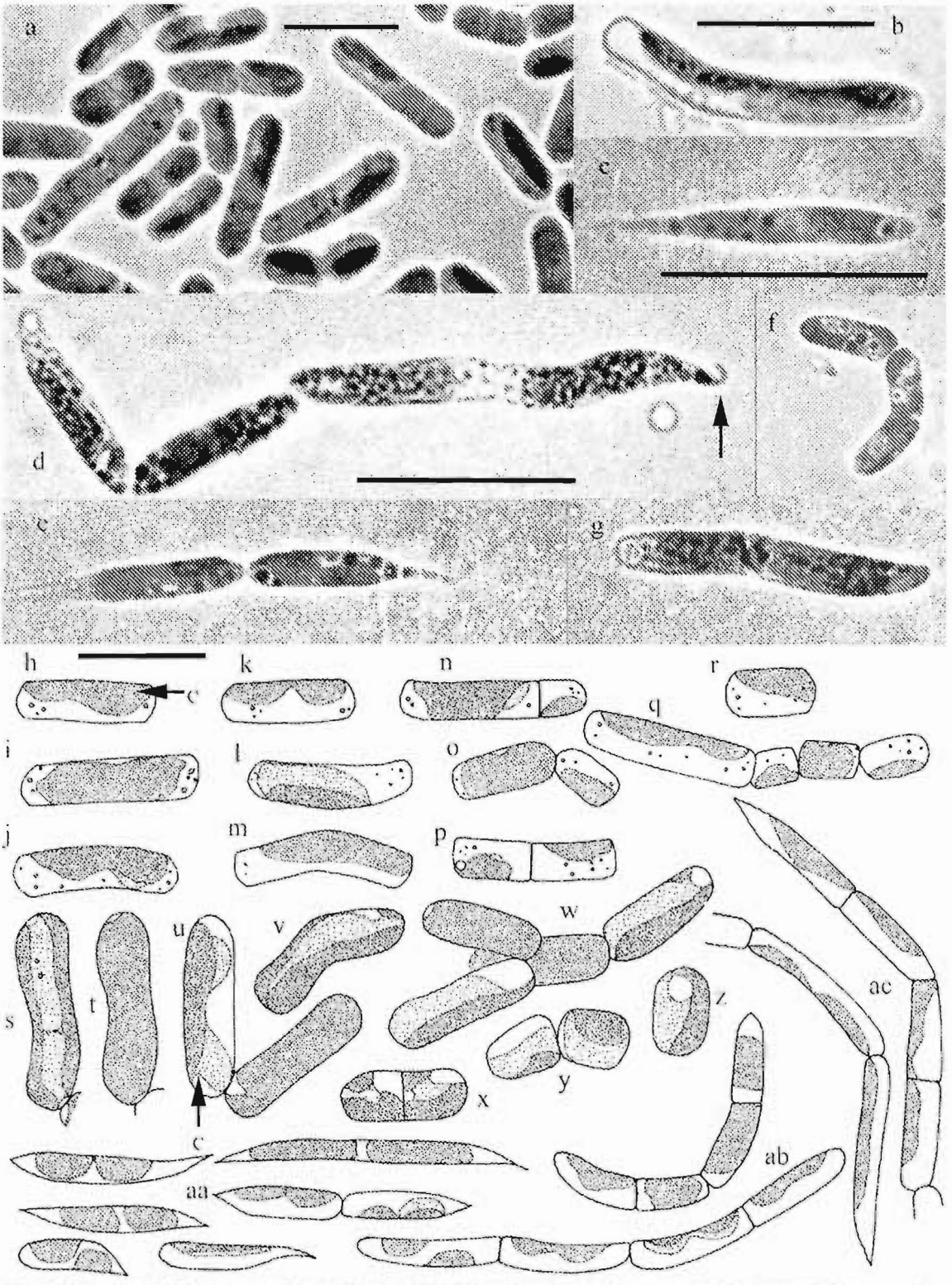


Fig. 6.25. a, h-r, *Stichococcus* cf. *bacillaris*, agarised culture material: a, vegetative cells; h-l, commonly observed cell shapes (C=chloroplast); m, more rarely observed bent cell; n-o, most common division pattern producing daughter cells of unequal length; p, more rarely observed division producing equal length daughter cells; q, typical short filament; r, cell released from fragmentation of filament.

b, s-z, *Stichococcus* cf. *mirabilis*, agarised culture material: b, vegetative cell; s, optical section of cell; t, surface view; u, common pattern of attachment of cell pairs (C=chloroplast); v, bent cell; w, cell group; x-z, cell division.

c-g, aa-ac, *Raphidonema nivale*, liquid culture material: c, e, cells resembling *Koliella*; aa, variation in morphology. Agarised culture material: d, mature filament showing hooked, attenuated apices (arrow); f, g, young cells resembling *Stichococcus*; ab, *Stichococcus*-like filaments; ac, classic *Raphidonema* morphology.

All scales=10 µm (use scale in d for d-g, h for h-ac).

(n=20). Chloroplast single, parietal, lacking lobes and incisions, lying along whole of one side of cell (Fig. 6.25h) or towards one end (Fig. 6.25l, m). At least one cell pole is usually clear of chloroplast and contains small granules. There may be a naked pyrenoid, but it is not easily visible in LM. Starch distributed evenly throughout chloroplast.

Reproductive features. Reproduction by vegetative division. New transverse wall usually more towards one cell pole, creating two daughter cells of unequal length (Fig. 6.25n). Division can result in chains of up to 4 (very rarely 5) cells (Fig. 6.25q), beyond which the filaments disintegrate. Onset of division is often in a slightly curved cell.

Remarks. Ettl and Gärtner (1995) report *S. bacillaris* to be straight cylindrical, whereas curved cells are occasionally observed in the Mt Philistine strain. However, since these curved cells are usually restricted to cells undergoing division (unlike in *S. allas*, where they are common), the alga has been assigned to *S.* cf. *bacillaris*. The length:width ratio of the cells is not useful for identification, as its range bridges those of several species of *Stichococcus* (Ettl and Gärtner 1995).

Stichococcus bacillaris is widespread in terrestrial and aerophytic environments (Ettl and Gärtner 1995). In New Zealand, it has been reported in the Waitomo Caves, Taupo, Tekoa, and Omarama soils (Cassie 1984), and on peat surfaces underlying *Olearia lyalii* vegetation, Snares Island (Flint and Fineran 1969).

***Stichococcus* cf. *mirabilis* Lagerheim** Fig. 6.25b, s-z.

Ettl and Gärtner (1995) p606-607, Fig. 204j.

Distribution. P, MF, SO, LM (MC)

Vegetative features. Filaments up to approximately 10 cells in length (Fig. 6.25w). Cells cylindrical, straight to slightly curved, often slightly tapered towards one pole (Fig. 6.25w) or slightly wider at both poles (Fig. 6.25s, t). Adult cells 10-15 µm long, 4-5 µm wide (length:width ratio = 1.6-3.8). Young cells 8-10 µm long, 3-5 µm wide. Chloroplast parietal, may encircle almost entire cell lumen or clearly be on one side of cell; lobes and incisions sometimes present (Fig. 6.25u). Pyrenoid absent. Cell wall smooth and thin.

Reproductive features. New transverse wall forms centripetally to give two daughter cells of equal size (Fig. 6.25x-z). Daughter cells become aligned at approximately 45°

to one another soon after division (Fig. 6.25u), giving rise to a bent and twisted filament which is readily fragmented.

Remarks: Slightly curved cells and swollen poles, cell width, and the lack of a visible pyrenoid under LM most resemble *Stichococcus mirabilis*. However, adult cells are considerably shorter than longest reported, and new transverse wall formed in vegetative division occurs in the middle of the cell rather than towards one end. Without TEM or molecular studies it cannot be determined for certain that the alga belongs to the Klebsormidiophyceae, and the genus *Stichococcus* probably requires revision.

S. mirabilis is reported from tree bark (Ettl and Gärtner 1995), a different habitat from that of the present specimens. It has not been included in New Zealand species lists (Cassie 1984).

Class Zygnemaphyceae

Order Zygnematales

Family Mesotaeniaceae

***Cylindrocystis brebissonii* var. *minor* West & West** Fig. 6.26a-c, i, j.

Croasdale and Flint (1988) p34, Fig. 1:17-1:20.

Distribution MF, P, SO, LM, HM (DE, EC)

Vegetative features. Cells single, cylindrical with rounded apices, approximately 47 µm long, 12 µm wide (3-4X longer than broad). Chloroplasts axial, with ridged surface (Fig. 6.26a, i), two per cell, each containing one central pyrenoid (Fig. 6.26i).

Reproductive features. None observed.

Remarks. This alga is assigned to *C. brebissonii* var. *minor* because it is less than 15 µm wide and is 3-4X longer than broad.

This variety is recorded as widespread in "acid places" in New Zealand (Croasdale and Flint 1988), including Whangamaino Swamp, Elstow Ponds, Moanatuatua Swamp (Hamilton), Otaki Swamp, and Addison's flat (Cassie 1984).

***Cylindrocystis crassa* cf. var. *elliptica* West & West** Fig. 6.26d-f, k-m.

Croasdale and Flint (1988) p35, Fig. 1:23.

Distribution. SO, P, LM, LV (DE, EC)

Vegetative features. Cells single, 30-35 μm long by 23-26 μm wide, ellipsoidal to cylindrical with broadly rounded ends (Fig. 6.26d), sometimes almost spherical (Fig. 6.26e). Chloroplasts axile, stellate, 2 per cell; pyrenoids central within chloroplasts, 2 per cell (Fig. 6.26k-l).

Reproductive features. Simple division (Fig. 6.26f, m). No sexual reproduction observed.

Remarks. This alga has a length:width ratio slightly greater than that of 1.0-1.2 reported for *C. crassa* var. *elliptica* by Croasdale and Flint (1988), but is below the range of 1.5-2.0 reported for var. *crassa*. It is within the size range reported for var. *elliptica*, but has 2 chloroplasts per cell rather than one, and also has a pyrenoid in each chloroplast. It could not be established whether the chloroplast has a toothed margin, as reported for var. *elliptica*, due to accumulation of oil globules inside the cells.

C. crassa var. *elliptica* has been reported in New Zealand from wet rocks and in swamps in the North Island (Croasdale and Flint 1988), including Tongariro National Park (Chapman *et al.* 1957) and Okarito Swamp (Cassie 1984).

cf. *Mesotaenium* Nägeli Fig. 6.27e, t-w.

Croasdale and Flint (1986) p29, 31. Ettl and Gärtner (1995) p611.

Distribution. P, MF, LM, LV (DE, EC)

Vegetative features. Cells solitary, cylindrical with rounded ends, 23-35 μm long, 18-22 μm wide. Cell wall smooth. Chloroplast plate-like, axial, y or x-shaped in transverse section (Fig. 6.27w), with 2-4 lobes running longitudinally along the cell (Fig. 6.27e, u), sometimes with a serrated margin (Fig. 6.27t). Pyrenoids absent.

Reproductive features. Not seen, although the shorter ("half-length") cells observed (Fig. 6.26t, v) are presumably the result of simple division.

Remarks. Non-ornamented cell wall, lack of median constriction, and plate-like axial chloroplast, are characteristic of *Mesotaenium*. However, radiating arms of chloroplast

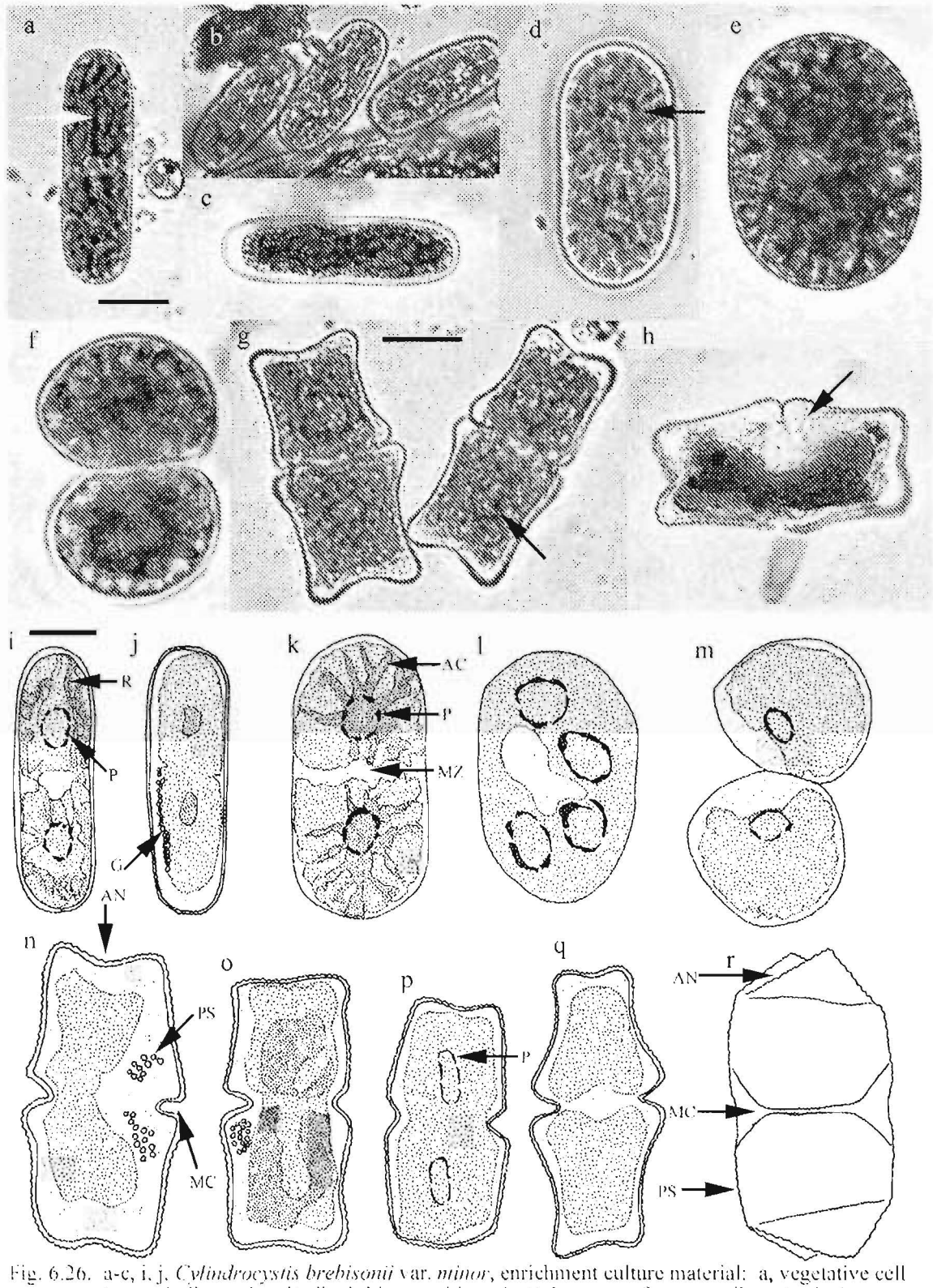


Fig. 6.26. a-c, i, j, *Cylindrocystis brebisonii* var. *minor*, enrichment culture material: a, vegetative cell (arrow indicates longitudinal ridge on chloroplast); b, group of young cells; c, typical appearance in field material; i, cell showing pyrenoid (P) and ridges (R) on chloroplast. Field material: j, cell with granules (G, small section shown) in cytoplasm.

d-f, k-m, *Cylindrocystis crassa* var. *elliptica*, enrichment culture material: d, young cell (arrow indicates pyrenoid in asteroidal chloroplast); e, mature cell; f, dividing cell; k, cell showing two asteroidal chloroplasts (AC), pyrenoid (P), and clear median zone (MZ); l, cell with 4 pyrenoids (possibly a newly formed zygote); m, cell division.

g, h, n-r, *Cosmarium decedens* var. *decedens*, enrichment culture material: g, rare cells with contents discernible (arrow indicates pyrenoid); h, cell with contents displaced to show punctate surface; n-q, variation in size and shape (AD=apical depression, MC=median constriction, PS=punctate surface, P=pyrenoid); r, rare side view of cell showing the same external features.

All scales=10 μm (use scale in a for a-f, g for g-h, i for i-r).

when seen in transverse section and absence of pyrenoids are both features preventing confident assignment to this genus (Croasdale and Flint 1986, Ettl and Gärtner 1995).

Mesotaenium is usually found in aquatic or subaerial habitats (Croasdale and Flint 1986).

Mesotaenium chlamydosporum* De Bary var. *chlamydosporum Fig. 6.27b, c, j-n.

Ettl and Gärtner (1995) p612-613, Fig. 207b. Croasdale and Flint (1986) p31, Plate 1 Fig. 1-2.

Distribution. SO, P, MF, LM, LV (DE, EC)

Vegetative features. Cells single, straight cylindrical with rounded ends, 16-22 μm long, 10-12 μm wide (length: width = 1.5-2.2); sometimes surrounded by mucilage (Fig. 6.27b), 5-10 μm thick. Cell wall smooth. Cell sap clear. Chloroplast an axial flat plate with 1 central pyrenoid (Fig. 6.26c).

Reproductive features. No zygospores observed.

Remarks. Size and length:width ratio, colourless cell sap, and smooth margin of the chloroplast assign the alga to *M. chlamydosporum*. The alga conforms well to the size range reported by Croasdale and Flint (1986) for *M. c.* var. *chlamydosporum*. It can be separated from the other two species of *Mesotaenium* on Mt Philistine by its smaller size, the large size of the pyrenoid relative to the size of the cell, and the smooth margin of the chloroplast.

M. chlamydosporum has been reported from Okarito Swamp, New Zealand (Cassie 1984).

Mesotaenium macrococcum* (Kűtzing) Roy & Bisset var. *macrococcum Fig. 6.27d, o-s.

Ettl and Gärtner (1995) p612-613, Fig. 207e. Croasdale and Flint (1986) p32, Plate 1 Fig. 7-9.

Distribution. SO, LM, LV (DE, EC)

Vegetative features. Cells single, straight cylindrical with rounded ends (Fig. 6.27d), 34-41 μm long, 17-20 μm wide (length: width = 1.9-2.4). Cell wall smooth. Cell sap

colourless. Chloroplast an axial flat plate with slightly toothed margin (Fig. 6.27d). Pyrenoid single, located midway along longitudinal axis but varying across width of chloroplast (Fig. 6.27q, s).

Reproductive features. Zygospores not observed.

Remarks. Size and length:width ratio, colourless cell sap, and rough margin of the chloroplast assign it to *M. macrococcum*. It is closest to *M. m.* var. *macrococcum* in size. Size range is at upper end of range described by Ettl and Gärtner (1995), and is close to that reported for *M. m.* var. *macrococcum* by Croasdale and Flint (1986). The latter authors do not mention the number of pyrenoids per cell; however all their illustrations show two pyrenoids. According to Ettl and Gärtner (1995), *M. macrococcum* may have one or two pyrenoids.

M. m. var *macrococcum* has been reported from moist soils and mosses in New Zealand (Croasdale and Flint 1986), including in Okarito Swamp (Cassie 1984).

Family Desmidiaceae

Cosmarium decedens* (Reinsch) Racib. var. *decedens Fig. 6.26g, h, n-r.

Croasdale and Flint (1988) p63, Fig. 37:22.

Distribution. LM, LV, SO, MF (DE, EC)

Vegetative features. Cells solitary, approximately 2X longer than wide, small constriction at sinus in top view (Fig. 6.26g, h, n-q), slightly depressed at apices, ovate-elongate in side view (Fig. 6.26r), semicells approximately trapeziform (Fig. 6.26n). Cell wall punctate (Fig. 6.26h) except in region of constriction. Cell width 12-20 µm at apex, 21-26 µm at basal lobe, 12-19 µm at constriction; 40-46 µm long; ~25 µm thick. Pyrenoids located centrally in each semicell (Fig. 6.26g, p).

Reproductive features. None observed.

Remarks. Semirectangular shape of semicells, the cell length, depressed apex, and open notch at the sinus, place this alga in *C. decedens*. *C. decedens* var. *decedens* has a punctate cell wall, the cell wall of *C. decedens* being smooth. Cell shape is exactly as illustrated by Croasdale and Flint (1988) for *C. decedens* in top view, and probably also in end view (no end views of the specimens were observed).

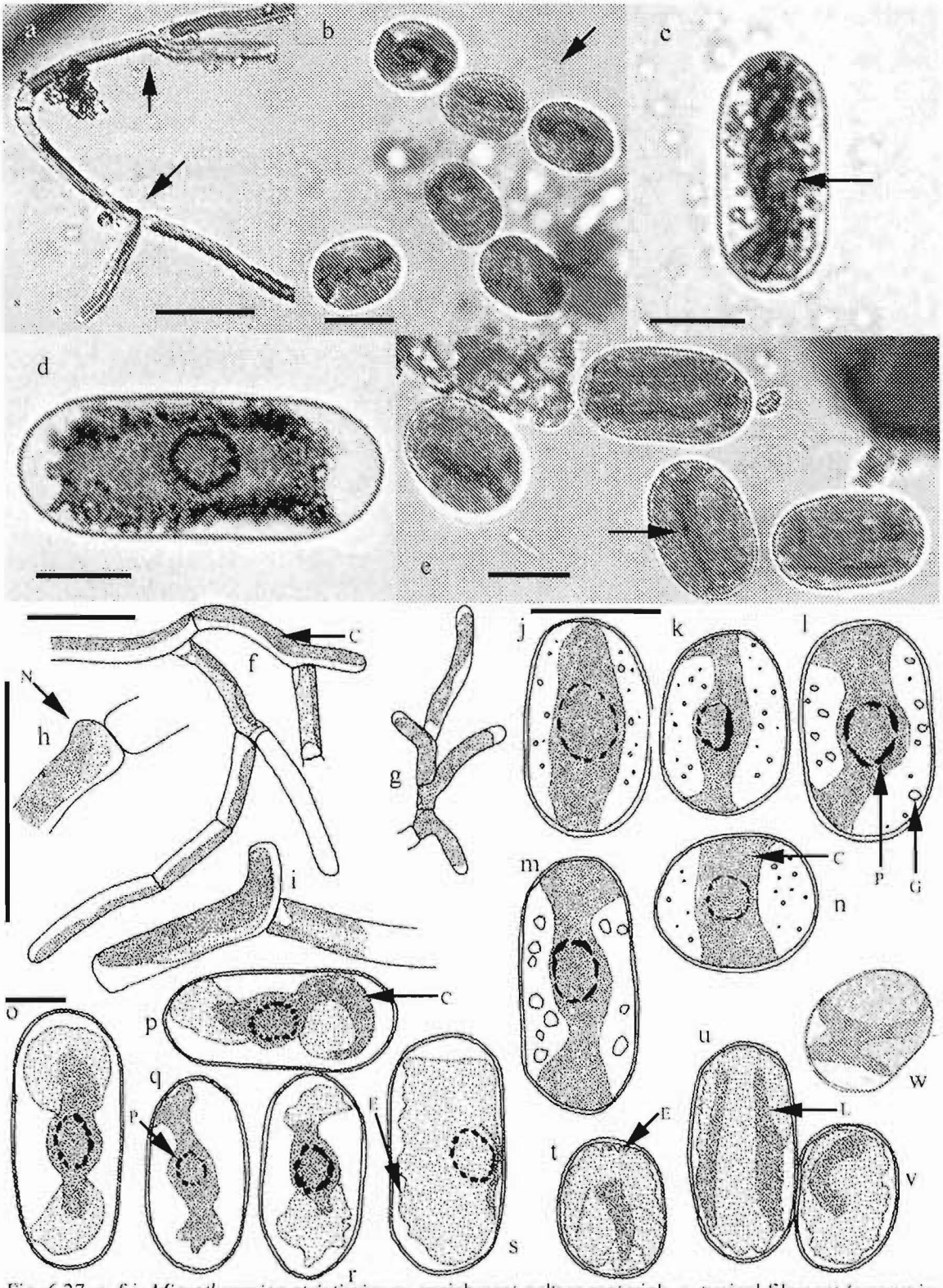


Fig. 6.27. a, f-i, *Microthamnion strictissimum*, enrichment culture material: a, typical filament (arrows indicate branch points); f, typical filament (C=chloroplast); g, developing filament with frequent branches; h, development of new branch (N); i, further growth of a new branch.

b, e, j-n, *Mesotaenium chlamydosporum* var. *chlamydosporum*, enrichment culture material: b, cell group surrounded by mucilage (edge indicated by arrow); e, single cell with mucilage absent (arrow indicates pyrenoid); j-m, variation in cell and chloroplast shape in longitudinal optical section (P=pyrenoid, G=cytoplasmic granules); n, transverse section (C=chloroplast).

d, o-s, *Mesotaenium macrococcum* var.*macrococcum*, enrichment culture material: d, single cell from enrichment culture; o-r, cell and chloroplast shape variation in longitudinal section (P=pyrenoid, C=chloroplast); s, opposing view of chloroplast (E=serrated edge).

e, t-w, cf. *Mesotaenium*, enrichment culture material: e, group of cells (arrow indicates longitudinal lobe on chloroplast); t,v, short cells resulting from division (E=serrated edge of chloroplast); u, typical cell (L=lobe on chloroplast); w, oblique view showing chloroplast cross section.

All scales=10 μm (use scale in f for f-g, h for h-i, j for j-n, o for o-w).

C. decedens var. *decedens* is found mostly in subaerial habitats, on wet rocks between mosses, and is widespread, especially in Arctic-alpine regions (Croasdale and Flint 1988).

Family Zygnemataceae

Zygnemataceae sp.1 Fig. 6.28a.
Ettl and Gärtner (1995) p637, Fig. 215e-f.
Distribution: MF (DE)

Vegetative features. Filaments uniseriate, unbranched, approximately 17 μm wide, with thick (1 μm) sheath (Fig. 6.28a). Cells cylindrical, 20-25 μm long, with very broadly rounded ends. Chloroplasts large, axial, possibly asteroidal, one in each half of cell.
Reproductive features. Not observed.
Remarks. This alga belongs to either *Zygnema* Agardh or *Zygogonium* Kűtzing. However, distinguishing between these genera requires observation of the zygospore, which is cut off from the vegetative cells by an extra wall in *Zygogonium*. Thus more specimens are required (only one filament was observed during the survey) to identify the alga to genus level.

Class Ulvophyceae
Order Pleurastrales
Family Pleurastraceae

***Microthamnion strictissimum* Rabenhorst** Fig. 6.27a, f-i.
Ettl and Gärtner (1995) p584-585, Fig. 197c,d.
Distribution. SO, MF, R, LV, LM (DE, EC)

Vegetative features. Filaments irregularly branched (Fig. 6.26f); each branch forms by lateral growth of a cell apex (Fig. 6.26h-i), resulting in a cell bent at ±45° at branch points (Fig. 6.26g); other cells straight to slightly curved. Cells 15-32 μm long, 3-4 μm

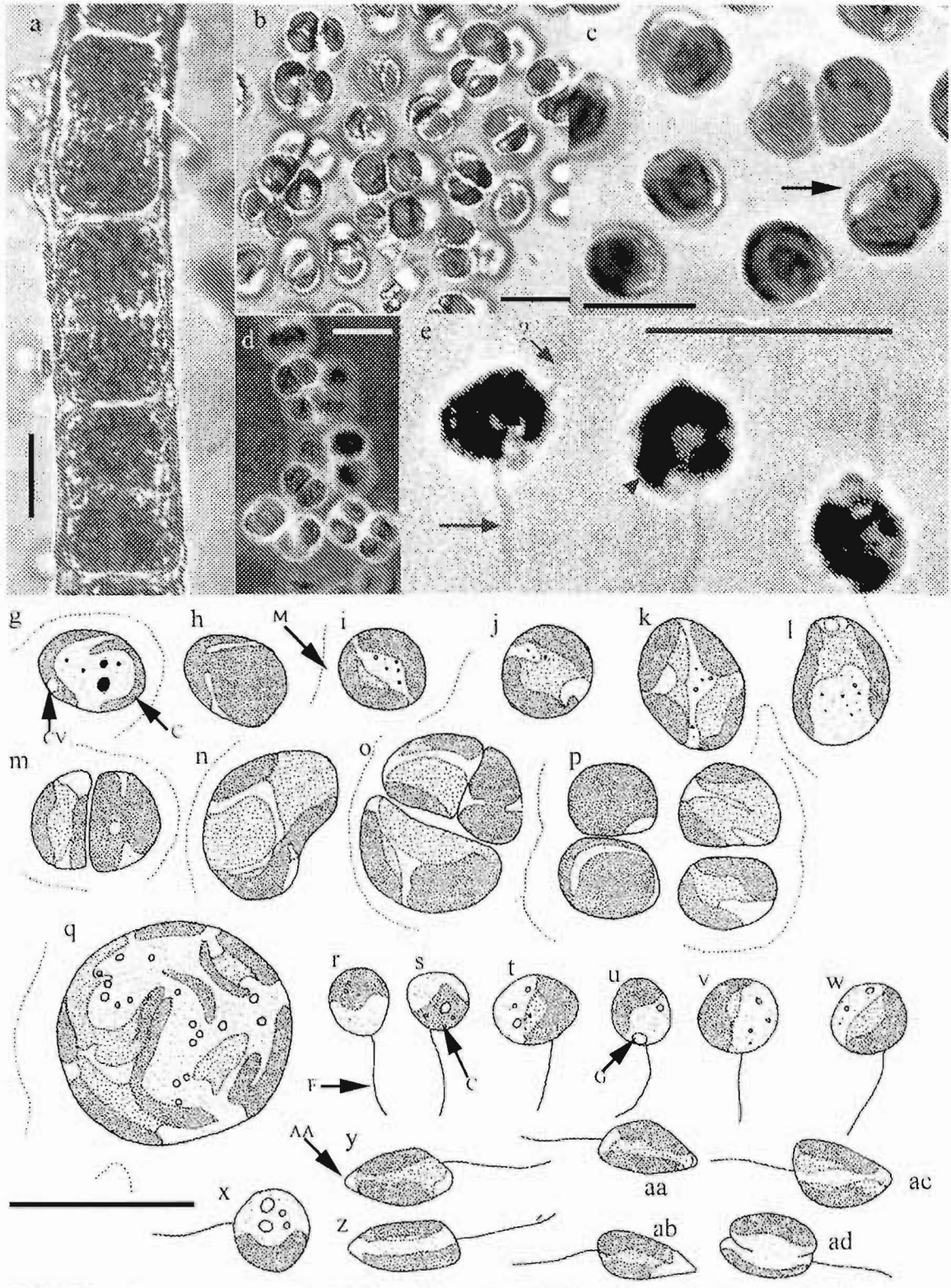


Fig. 6.28. a, Zygnemataceae sp. 1, field material: portion of filament (arrow indicates chloroplast).

b-d, g-q, *Chrysosaccus* cf. *epilithicus*, agarised culture material: b, c, mucilaginous colony (arrow indicates dividing cell); d, Indian ink preparation showing mucilage; g, cell in optical section (CV=contractile vacuole, C=chloroplast); h, same cell in surface view, showing bilobed chloroplast; i-l, variation in chloroplast shape; m, recently divided cell pair; n, cell with divided chloroplast; o, cell division; p, cell tetrad resulting from two divisions; q, giant cell rarely observed in culture.

e, r-ad,, *Chromulina* cf. *elegans*, liquid culture material: e, cells preserved in Lugol's iodine (arrow to flagellum, arrowhead to chloroplast, ?=possible second flagellum; r-x, variation in cell and chloroplast shapes (F=flagellum, C=chloroplast, G=granules in cytoplasm); y-ac, cells several months old (AA=attenuated apex); ad, dividing cell.

All scales=10 µm (use scale bottom left for g-ad).

wide (length:width = 3.8-8.0). Chloroplast parietal, enclosing about half cell circumference (Fig. 6.26f), lying along only one side of cell or sometimes twisted.

Reproductive features. Filament readily fragments.

Remarks. The alga is assigned to *M. strictissimum* because its cell dimensions and length:width ratio are almost exactly those specified by Ettl and Gärtner (1995).

In New Zealand, *M. strictissimum* has been found in Deepwater Cove (Kaipara Harbour), Otaki Swamp (Murchison), Okarito, Lake Matheson (Westland National Park), Lake Dispute and Swampy Hill Pond, Dunedin (Cassie 1984).

Division Heterokontophyta

Class Chrysophyceae

Order Chrysocapsales

***Chrysosaccus* cf. *epilithicus* Starmach** Fig. 6.28b-d, g-q.

Starmach (1985) p417 Fig. 885.

Distribution. SO (MC)

Vegetative features. Colonies large, with cells commonly arranged in flat aggregates of 4 or in cubical aggregates of 8 throughout colourless homogeneous mucilage (Fig. 6.28p). Cells broadly ellipsoidal to spherical (Fig. 6.28b-d). Adult cells 7-11 μm long, 5-9 μm wide. Chloroplast golden-brown, parietal, one or two per cell, bilobed with deep incisions (Fig. 6.28g-p). Single contractile vacuole present (Fig. 6.28g). Pyrenoid, stigma and cell wall absent. Occasional giant spherical cells produced, 15-18 μm wide, with 5 or more chloroplasts (Fig. 6.28q).

Reproductive features. Division in up to three planes, giving cubical aggregates of 8 cells. Daughter cells 5-7 μm long, 3-5·μm wide. Zoospores not observed.

Remarks. Characteristic flagellar features of the Heterokontophyta cannot be observed in this non-motile species. Palmelloid form and the lack of flagella and zoospores place it in the subclass Acontochrysophycidae, order Chrysosaccales. It belongs to *Chrysosaccus* due to mucilaginous, irregularly-shaped colonies and 4-cell aggregates. It is possible that the 8-cell aggregates have previously been missed when observing this poorly-known genus. It is assigned to *C. epilithicus* on account of its size range and the presence of one or two chloroplasts per cell, which lack a stigma. The generic diagnosis

(Starmach 1985) states that a stigma is present, but only one of the three described species is reported to have a stigma. The occasional giant cells found in the Mt Philistine specimens were not described by Starmach (1985), but may be bizarre forms associated with culturing.

C. epilithicus has been reported from rock surfaces in streams in Europe (Starmach 1985). It has not been included in New Zealand species lists (Cassie 1984).

Order Chromulinales

***Chromulina* cf. *elegans* Doflein** Fig. 6.28e, r-ad, Fig. 6.29.
Starmach (1985) p45, Fig. 25. Stein (1963) p1367-1370.
Distribution. SN (DE, MC)

Vegetative features. Young cells spherical to ellipsoidal, 4.5-7.0 μm long, 4.5-6.0 μm wide; chloroplast single (Fig. 6.28r-x). Old cells elongate to spindle shape (Fig. 6.28y-ac), 8.0-9.0 μm long, 4.0-6.0 μm wide, with 1-2 chloroplasts. Cell wall absent. Anterior (long) flagellum 6.0-9.0 μm long (Fig. 6.28e, r); short flagellum arising perpendicular to this, not visible in LM but base observed in TEM (Fig. 6.29b, e). Chloroplast golden-brown, parietal, cup-shaped; thylakoids arranged in stacks of three (Fig. 6.29c) with girdle lamella outermost. Genophores present at chloroplast poles (Fig. 6.29d).
Reproductive features. Cells divide longitudinally (Fig. 6.28ad).
Remarks. Assignment to the Heterokontophyta is confirmed by thylakoids in stacks of three and presence of genophores in the chloroplast. According to the system of Starmach (1985), the alga is placed in Heterochrysophycidae because it is unicellular, and in Chromulinales, suborder Chromulineae, because it has one flagellum visible in LM and lacks a cell wall. The predominance of a motile stage, the number of chloroplasts, and the lack of any type of envelope surrounding the cells places it in family Chromulinaceae. Absence of surface structures and chloroplast shape and number assign it to *Chromulina*. Shape of the young cells is most similar to the published description of *C. elegans* (Starmach 1985), although this is reported to be half the size of the present strain with a relatively shorter flagellum visible in LM. Although *Chromulina* has previously been distinguished from *Ochromonas* on the basis of

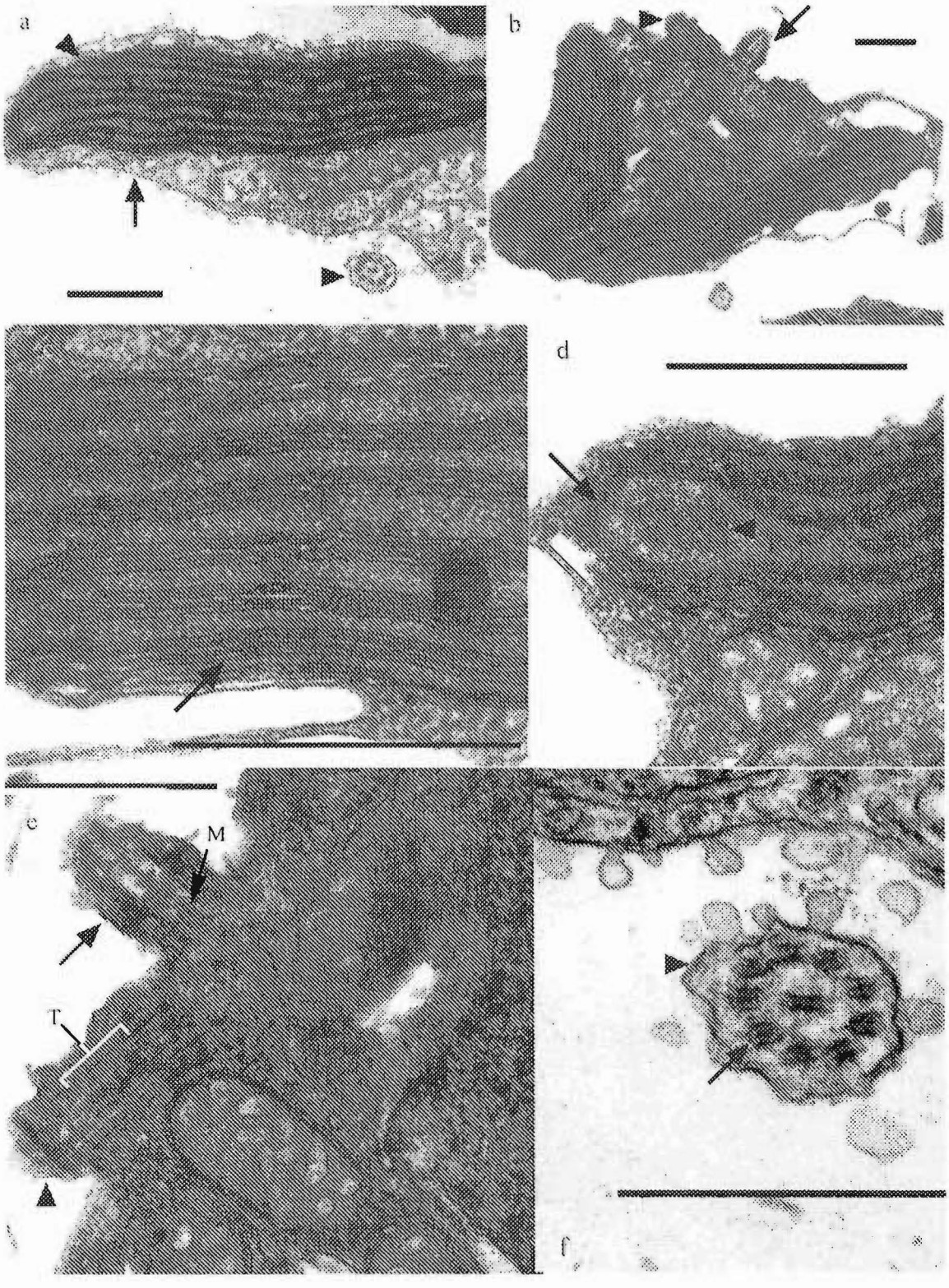


Fig. 6.29. *Chromulina* cf. *elegans*, TEM of liquid culture material: a, half cell showing plasmalemma (arrow), chloroplast (arrowhead, top) and transverse section of flagellum (arrowhead, bottom); b, whole cell showing bases of long (arrow) and (probably) short flagellum (arrowhead) at right angles; c, detail of chloroplast showing thylakoids (arrow) in stack of three; d, detail of chloroplast showing genophore (arrowhead) and probable girdle lamella (arrow); e, detail of long (arrowhead, top) and short or posterior (arrowhead, bottom) flagella bases (M=microtubules, T=transitional region); f, transverse section through flagellum (arrow indicates microtubules, arrowhead indicates membrane).

All scales=500 nm.

number of flagella, modern systems group these genera on the basis that many *Chromulina* species have been found to have a short flagellum not visible in LM (Preisig 1995). The alga still belongs in the Chromulinaceae according to modern systems because there is no evidence for scales covering the cells. Alternative species placements could be *C. slavaca* Juris, which has a similar appearance to old cells but not young cells, or *C. minima* Doflein, which has ellipsoidal cells which are too small (2-3μm long) to be considered.

This alga is not the snow alga *C. chionophila* Stein because it is not flattened in cross-section and has fewer chloroplasts than the 2-3 per cell reported by Stein (1963).

C. elegans has been reported from pond waters in Europe. It has not been included in New Zealand species lists (Cassie 1984).

Chrysophyceae, uncertain assignment

Chrysophyceae sp 1 Fig. 6.30a-k.
Fogg (1967) p279-287.
Distribution. SN (DE)

Features. Cells spherical, 12-25 μm diameter; surrounded by 2 envelopes in young cells (Fig. 6.30a). Inner envelope against cell wall except where it forms a spout, piercing outer envelope approximately 3 μm from cell wall (Fig. 6.30e). Spout cylindrical, may be slightly broader at apex and base (Fig. 6.30f, h), 3-4 μm wide, 5-8 μm long, composed of inner and outer tubes (Fig. 6.30b, d). Outer envelope lost in older cells (Fig. 6.30c, g-k). Central structure, probably nucleus, visible in preserved material (Fig. 6.30e). Chloroplast usually fragmented, occasionally complete and possibly asteroidal (Fig. 6.30j, k); little internal detail visible due to masking red pigment.

Remarks. This alga is characteristic of a chrysophycean cyst, such as that of *Chromulina rosanoffii* Bütschli, which has a shorter spout. It is possible that *Chromulina* cf. *elegans* constitutes its vegetative state. However, the distribution of the two cell types appears almost mutually exclusive – the flagellate has been recorded in high numbers from tarn snow, and the cyst is far more common on snow elsewhere. If this cyst was formed from *Chromulina* cf. *elegans*, high numbers of cysts would be expected in tarn snow by the end of the growing season.

The closest report of a similar organism from snow is that of Fogg (1967), who recorded a "spouted red cell" of 4.5-9.0 μm diameter, with a single parietal greenish-yellow chloroplast lacking starch, from snow in the South Orkney Islands, Antarctica. No similar organism has been previously found in snow in New Zealand.

Class Bacillariophyceae
Order Pennales
Suborder Raphidineae
Family Naviculaceae

***Cymbella kapii* Cholnoky** Fig. 6.30n, o.
Foged (1979), p196, Plate XXXIV: 8-10.
Distribution. A (DE)

Features. Valves isopolar dorsiventral, semilanceolate, 27 μm long, 8 μm wide in valve view. Ends rostrate. Striae parallel near central area, radiate towards ends (changeover ratio 4/1); puncta equally spaced and clearly separated, approximately 15 per 10 μm. Central area undifferentiated. Raphe central, bent ventrally, undulate, threadlike; central terminals sickle-shaped, polar terminals bent ventrally (Fig. 6.30n). Two stigmata on ventral side of central raphe pores. Central nodule absent.
Remarks. Valve shape and size, striae pattern, raphe position and shape, and presence of two stigmata in the central area place the alga in *Cymbella kapii.*

The species is reported from freshwater in the North Island, New Zealand (Foged 1979).

***Gomphonema parvulum* Kützing** Fig. 6.31c.
Krammer and Lange-Bertalot (1997) p358-360, Fig. 154: 1-25.
Distribution. A (DE)

Features. Valves asymmetrical heteropolar, ovate; 18 μm long, 6 μm wide in valve view. Ends rostrate. Striae near-parallel throughout (Fig. 6.31c), approximately 15 per 10 μm; puncta equally spaced and clearly separate. Central area a 1-sided fascia with

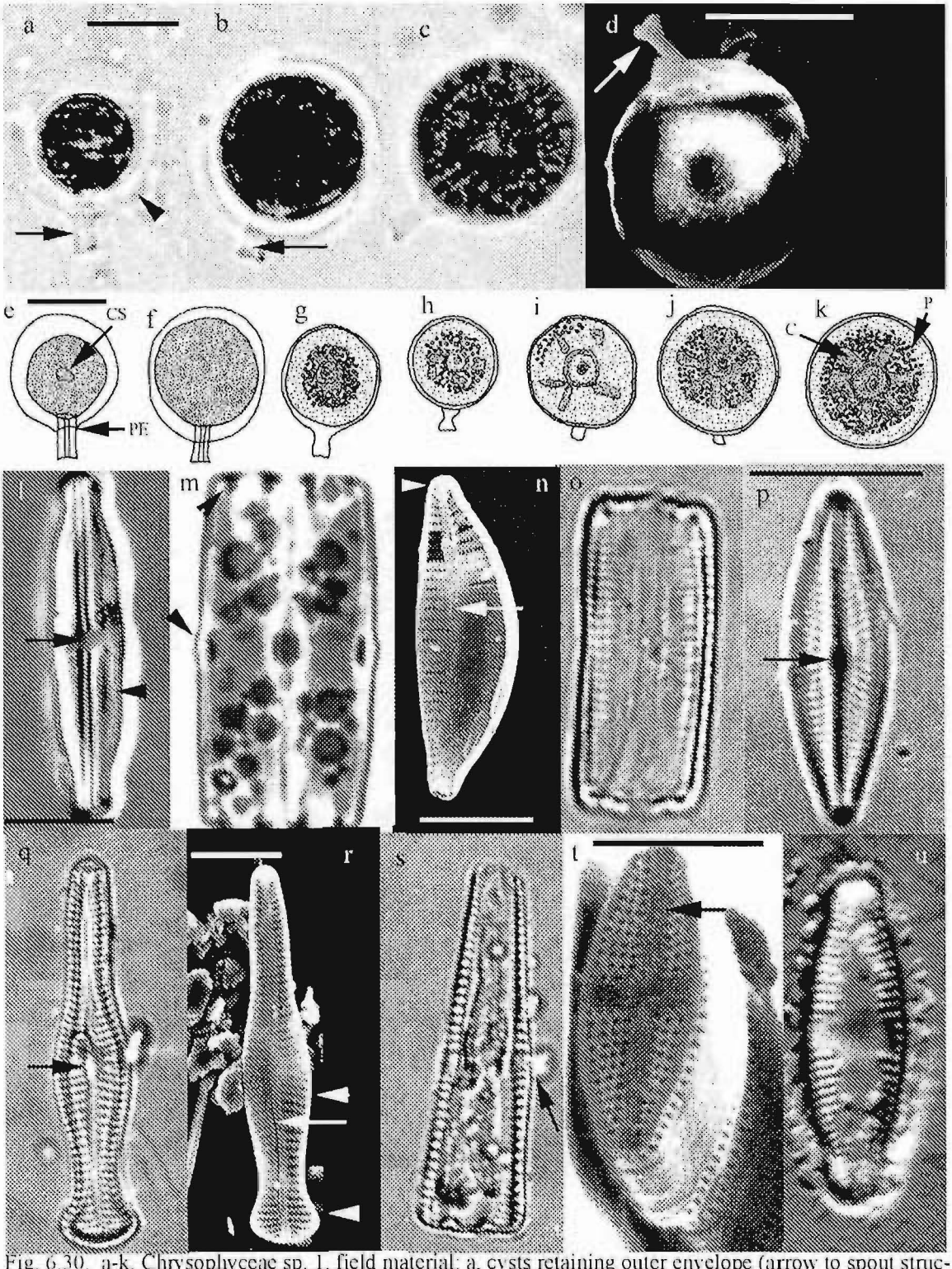


Fig. 6.30. a-k, Chrysophyceae sp. 1, field material: a, cysts retaining outer envelope (arrow to spout structure, arrowhead to envelope); b, cell showing inner tube of spout (arrow); c, mature cyst lacking outer envelope; d, SEM of mature cyst showing inner tube of spout indicated by arrow (outer layer of spout absent); e-f, cysts showing central structure (CS) and point of spout emergence through envelope (PE); g-k, variation in mature cysts (P=red pigment, C=chloroplast).

l, m, *Stauroneis* cf. *prominula*, enrichment culture material: l, Nomarski DIC, valve view (arrow to inflated central area, arrowhead to radiate striae; m, girdle view (arrowheads to silica thickenings).

n, o, *Cymbella kapii*, field material: n, SEM, valve view (arrow to raphe, arrowhead to sickle-shaped terminal); o, Nomarksi DIC, girdle view.

p, *Navicula* sp., field material: Nomarski DIC, valve view (arrow to circular central area).

q-s, *Gomphonema truncatum*, field material: q, DIC, valve view (arrow to elongate central area); r, SEM, valve view (arrow to undulating raphe, arrowheads to radiate (top) and parallel striae); s, DIC, girdle view (arrow to inflated central nodule).

t, u, cf. *Achnanthes*, enrichment culture material: t, SEM, valve view (arrow to pseudoraphe); u, DIC, valve view.

All scales=10 µm (use scale in a for a-c, e for e-k, l for l-m, n for n-o, r for q-s, t for t-u).

single stigma at terminal of central stria (Fig. 6.31c). Raphe simple, threadlike; central terminals simple, polar terminals sickle-shaped. Axial area linear. Central nodule absent.

Remarks. The near-isopolarity in valve view, stigma and absent stria on opposite sides of the central node, and size place the alga in *G. parvulum.*

The species has been recorded from stagnant fresh and brackish water in the North Island, New Zealand (Foged 1979).

***Gomphonema truncatum* Ehrenberg** Fig. 6.30q-s.

Krammer and Lange-Bertalot (1997) p369-370, Fig. 159:11.

Distribution. A (DE)

Features. Valves asymmetric heteropolar, clavate, isobilateral; 42 μm long, 8 μm wide at central swelling, 9 μm wide at capitate end. Narrow end rounded. Striae radiate around unilaterally gibbous central area, parallel at midpoints, radiate at ends, approximately 11 per 10 μm. Puncta equally spaced. Raphe undulate, threadlike; central terminals simple; polar terminals sickle-shaped. Axial area lanceolate; central nodule slightly inflated on hypovalve.

Remarks. Size, striae pattern and lack of a polar process on the capitate end place the alga in *G. truncatum.*

The species is reported as cosmopolitan in clean freshwater (Krammer and Lange-Bertalot 1997).

***Navicula* sp.** Fig. 6.30p.

Krammer and Lange-Bertalot (1997a) p84-85.

Distribution. A (DE)

Features. Valves symmetrical isopolar, wide lanceolate; 18 μm long, 6 μm wide in valve view. Ends rounded. Striae radiate around central area, parallel towards ends (changeover ratio 3/1), approximately 15 per 10 μm. Central area elliptical (Fig. 6.30p). Raphe simple, threadlike. Central nodule absent.

Remarks. Linear raphe, isopolar apical axis, visible puncta, elliptical central node and lack of raised ribs and septum assign the alga to *Navicula*. Puncta arrangement around the central area requires investigation to proceed further with identification.

***Stauroneis* cf. *prominula* (Grunow) Hustedt** Fig. 6.30l, m.
Krammer and Lange-Bertalot (1997a) p247, Fig. 90: 16-20 p621.
Distribution. SO (EC)

Features. Valves symmetrical isopolar, weakly triundulate, 25 μm long, 8 μm wide in valve view. Ends rostrate; striae probably radiate throughout; pores very fine. Central area a narrow transverse fascia. Raphe simple, threadlike, situated on raised linear axial ridge; central terminals simple and widely spaced; polar terminals slightly sickle-shaped. Central nodule bilaterally inflated; silica thickenings present beneath valve faces and around central area (Fig. 6.30m).
Remarks. Silica thickenings visible in girdle view, large gap between central raphe pores, weakly triundulate valve shape and radiate striae are characteristic of *Stauroneis prominula*..

The species is thought to be cosmopolitan in stagnant and running fresh water and has been reported in slightly brackish conditions (Krammer and Lange-Bertalot 1997).

Family Achnanthaceae

cf. *Achnanthes* Fig 6.30t, u.
Krammer and Lange-Bertalot (1991) p2.
Distribution. SO (EC)

Features. Valves symmetrical isopolar, wide lanceolate; 18μm long, 8μm wide in valve view. Ends rostrate; striae radiate throughout, approximately 13 per 10μm; puncta equally spaced and clearly separated. Central area a transverse fascia. Raphe absent, pseudoraphe linear, central nodule absent (information available for only the araphid valve face).

Remarks. Absence of a raphe on at least one of the valves places the alga in either suborder Raphidineae, family Achnanthaceae or suborder Araphidineae, family Fragilariaceae. The valve shape and pseudoraphe with fascia-shaped central area are more typical of an araphid valve in Achnanthaceae, and the rostrate ends would thus assign the alga to *Achnanthes*. Information on the opposing valve is required to confirm this identification and assign a species name.

Family Bacillariaceae

***Nitzschia* sp.** Fig. 6.31a.
Krammer and Lange-Bertalot (1997b) p8-9.
Distribution. A (DE)

Features. Valves symmetrical isopolar, acicular, 32 μm long, 3 μm wide in valve view. Ends rounded. Raphe eccentric, along one valve margin. Fibulae parallel, without central break or space, approximately 15 per 10 μm. Axial area linear, central nodule absent.
Remarks. Raphe position and location on valve surface places the alga in Bacillariaceae. Presence of fibulae, isopolar apical axis, and absence of septa assign it to *Nitzschia*. There is a large amount of variation, particularly in end structure, within and between species in this genus and more specimens are required for further identification.

Family Fragilariaceae

***Synedra ulna* (Nitsch) Ehrenberg var. *contracta* Østrup** Fig. 6.31b.
Foged (1979) Plate VIII: 9, 10.
Distribution. A (DE)

Vegetative features. Symmetrical isopolar, panduriform; 30 μm long, 4 μm wide at constriction in valve view. Ends narrowly rostrate. Striae parallel, approximately 16 per 10 μm. Raphe and central nodule absent. Axial area linear.

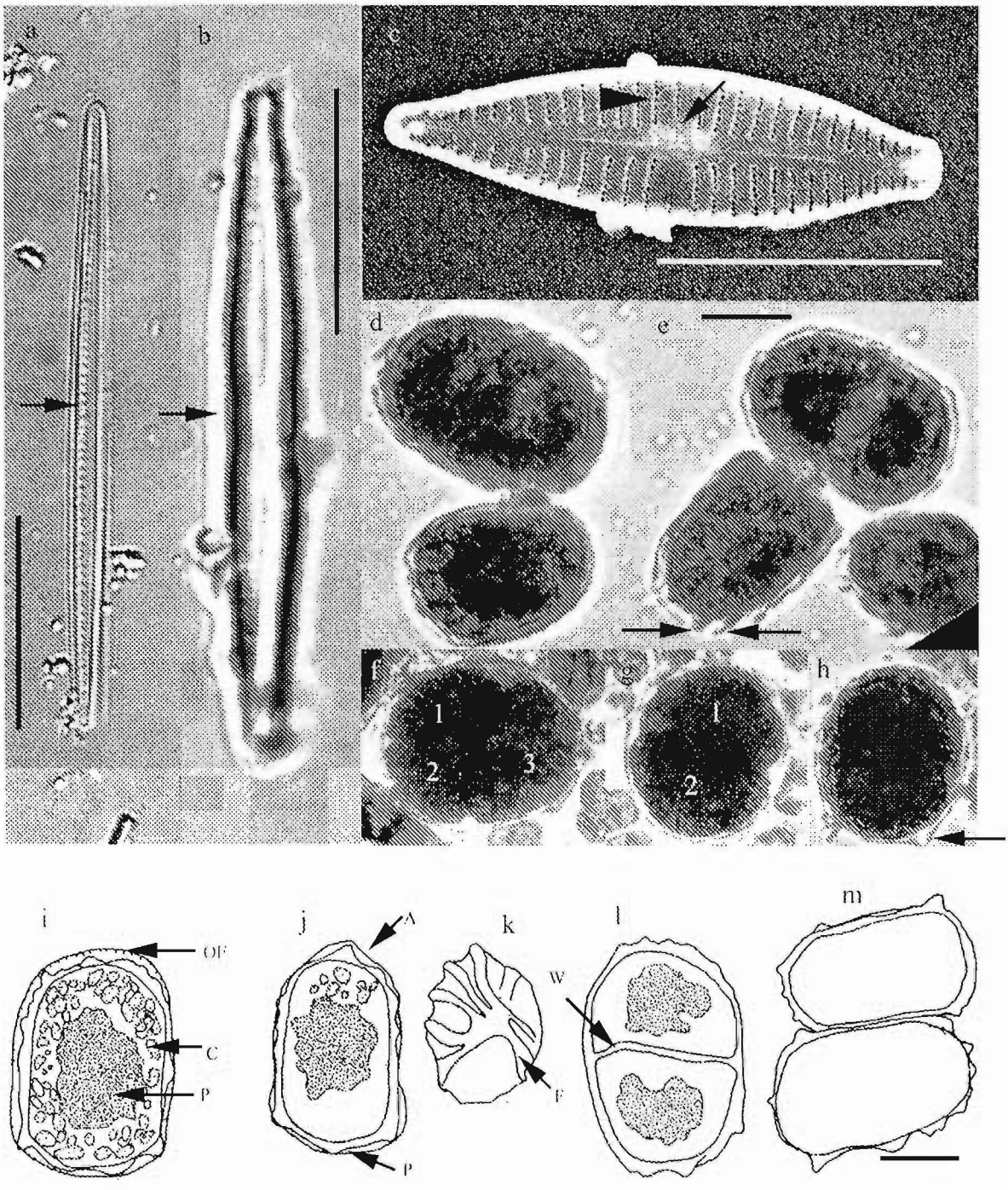


Fig. 6.31. a, *Nitzschia* sp, field material: Nomarksi DIC, valve view (arrow to eccentric raphe and fibulae).

b, *Synedra ulna* var. *contracta*, field material: Nomarski DIC, valve view (arrow to constriction at central area).

c, *Gomphonema parvulum*, field material: SEM, valve view (arrowhead to parallel striae, arrow to stigma).

d-m, Xanthophyceae sp.1, enrichment culture material: d, mature cell (top) and smaller cell resulting from a recent division; e, cell group with longitudinal flanges (arrows) visible on envelope; f, sporangium containing 4 autospores (1-3 numbered); g, 2-spore autosporagium; h, cell with distinctive lobe on envelope (arrow); i, cell with reduced red pigment (P), numerous yellow-green chloroplasts (C), and punctate outer envelope (OE, not always present) surrounding flanges; j, cell displaying distinctive polarity; k, appearance of flanges (F) under LM; l, division of cell into two daughter cells (W=new cell wall); m, two daughter cells (note opposite polarity).

All scales=10 μm (use scale in e for d-h, m for i-m).

Remarks. The parallel striae, small rostrate ends and slight constriction at the central area are characteristic of *Synedra ulna* var. *contracta*.

The species has been reported from lakes and rivers in the North Island, New Zealand (Foged 1979).

Class Xanthophyceae

Uncertain assignment

Xanthophyceae sp. 1 Fig. 6.31d-m.

Distribution. P, LM, LV (DE, EC)

Vegetative features. Cells ellipsoidal-cylindrical, tapered slightly towards one pole, 19-29 µm long, 12-18 µm wide. Cell contents largely obscured by dense red secondary pigment; where this retracts, numerous parietal discoidal yellow-green chloroplasts are visible (Fig. 6.31i). Cell surrounded by 1-2 envelopes. Inner envelope convoluted, forming flanges radiating generally towards narrower pole from a central point on the cell surface (Fig. 6.31e, k). Outer envelope (when present) smooth or lightly punctate (Fig. 6.31i).

Reproductive features. Autospores, 2-4 per sporangium (6.31f, g, l, m). Daughter cell pairs positioned in opposite orientation before separation (Fig. 6.31m).

Remarks. Yellow-green colour of chloroplasts, although these are seldom visible, forms the basis for placement in Xanthophyceae. The characteristic envelope structure seems to be unrecorded in the literature on the Xanthophyceae (e.g. Ettl and Reith 1978). Further description, especially by SEM, is hampered by difficulty in obtaining sufficient specimens.

6.4. Discussion

6.4.1. Summary of the Mt Philistine algal flora

Sixty-seven distinct taxa were identified from the alpine zone on Mt Philistine, comprised of 15 cyanophytes, 1 euglenophyte, 12 heterokontophytes, and 39

chlorophytes. The heterokont flora comprised 8 diatoms, 3 chrysophyceans, and 1 xanthophycean, and the chlorophytes included 7 desmid taxa.

Eight taxa are thought to be obligate snow algae. The spherical, mineral-coated red snow cysts, thought to be *Chlamydomonas* sp., may have been recorded previously from New Zealand (Thomas and Broady 1997), and the spouted cyst labelled Chrysophyceae sp. 1 has been found previously in the Arthur's Pass area (Broady pers. com.). *Chlainomonas kolii*, *Chloromonas rubroleosa*, *Chloromonas* sp. 2-4, and *Chromulina* cf. *elegans* are all new records for New Zealand. *Chloromonas* sp. 3 may represent the vegetative state of the previously described *Scotiella nivalis* var. *californica* (Kol 1968b). The new records of snow algae for New Zealand, and progress made in elucidating the life cycle of *Chlainomonas kolii*, were achieved only by combining culture work with exhaustive examination of field specimens. The importance of this approach has been demonstrated previously (Hoham 1975, Hoham and Mullet 1977, Hoham *et al.* 1979, 1983, Ling and Seppelt 1990, 1993, 1998a, b).

A ninth snow alga, *Raphidonema nivale*, which has probably been found previously in New Zealand (Thomas and Broady 1997), is regarded as facultative in snow (Fukushima 1963, Hoham 1971, 1973). However, it was never recovered from habitats other than snow on Mt Philistine (see Chapter 3).

Chloromonas sp. 2, Chrysophyceae sp. 1, and *Chromulina* cf. *elegans* may be new species of snow algae. Xanthophyceae sp. 1 is almost certainly a new species, and others may be cf. *Mesotaenium*, *Coccothrix* cf. *chlorolobata*, and cf. *Trochisciopsis tetraspora*. The snow algae, and also cf. *T. tetraspora*, require complete elucidation of their life-cycles to confirm new species status. Further TEM work and molecular genetics may be required to distinguish *C.* cf. *chlorolobata* from Antarctic *C. chlorolobata*. Given that *Chloromonas rubroleosa* from Mt Philistine has been implicated in a life-cycle involving *Chlainomonas kolii* cell types, a similar comparison with the original Antarctic cells could be revealing.

Forty of the 67 taxa have either been assigned species names only tentatively, or have been classified to genus only (rarely to class only). This includes 13 cyanophytes, 1 euglenophyte, 22 chlorophytes, 3 chrysophyceans, 1 xanthophycean, and 4 diatoms. The complete classification of these organisms awaits further studies of their ultrastructure and molecular genetics. Many differ in minor ways from published descriptions of traditional morphological characteristics, such as the occasional occurrence of curved cells of *Stichococcus* cf. *bacillaris*, and type of chloroplast

incisions in *Chlamydomonas* cf. *noctigama*. These features may be responses to different culture conditions used by different researchers. If they are not, do they constitute differences significant enough for erection of new species? This question reflects a need for greater taxonomic resolution, which molecular methods may provide (Graham and Wilcox 2000). Many of the common cyanophytes, such as *Fischerella* sp., cf. *Gloeocapsa*, and cf. *Ammatoidea*, require isolation into culture for their complete characterisation.

6.4.2. Comparison with algal floras from elsewhere

No flora reported from any other region is identical to that found on Mt Philistine. However, certain floras bear similarities which make a brief examination worthwhile.

Other alpine regions. Epilithic communities in the Maritime Alps, France (Fjerdingstad 1965) resemble those at Mt Philistine. Cyanophytes dominate these communities, including the genera *Gloeocapsa*, *Calothrix*, *Chroococcus*, *Microcoleus*, *Myxosarcina*, and *Nostoc*, which are shared with Mt Philistine. In the Swiss Alps, species found on all rock types which also occur in the Mt Philistine flora are *Cyanothece* (*Synechococcus*) *aeruginosa*, *Cylindrocystis brebissonii*, *Mesotaenium macrococcum* var. *macrococcum*, *Stichococcus bacillaris*, and *Klebsormidium* (*Hormidium*) *flaccidum* (Jaag 1945). In addition, the genera *Myrmecia*, *Scotiellopsis*, *Trochisciopsis*, and *Stichococcus* have been cultured from soils in the Dolomites, Italy (Vinatzer 1975).

Antarctica. Of the polar regions, Antarctica could be expected to have the most similar algal flora to New Zealand, due to its proximity. Algae from Mt Philistine which have been reported from Antarctica (Longton and Holdgate 1979, Seaburg *et al.* 1979, Broady 1979a, 1984, 1987a, b, 1989a, b, Broady and Ingerfeld 1999, Broady and Lokhorst 2000, Ling 1996, Ling and Seppelt 1990, 1993, 1998a, b, 2000, Ryan *et al.* 1991, Mataloni and Tesolin 1997, Ohtani *et al.* 1998) include *Phormidium* sp., *Pseudococcomyxa simplex*; *Stichococcus* cf. *bacillaris*, cf. *Ammatoidea*, *Coccomyxa* cf. *gloeobotrydiformis*, *Chloromonas rubroleosa*, *Chloromonas* sp.4 (*Scotiella antarctica*),

Chlamydocapsa sp., *Muriellopsis* cf. *sphaerica*, cf. *Oocystis minuta*, *Coccothrix* cf. *chlorolobata*, and *Raphidonema nivale*.

The dominant algae in the Marie Byrd Land flora are common to Mt Philistine. *Gloeocapsa* sp. is the most common epilith. *Cyanothece aeruginosa*, *Stichococcus bacillaris*, and *Pseudococcomyxa simplex* are dominant in other habitats (Broady 1989a).

A detailed survey of the Windmill Islands region has been completed, revealing 145 non-marine taxa, 24 of which occur in snow, and nearly half of these are obligate snow algae (Ling and Seppelt 2000). *Chloromonas rubroleosa*, an alga of red snow, is common to the Mt Philistine study site (see Chapter 4). Others are *Raphidonema nivale* from snow, cf. *Ammatoidea* from aquatic habitats, and *Pseudococcomyxa simplex* and *Stichococcus bacillaris* from terrestrial habitats (Ling and Seppelt 1998a). There are 13 genera in common.

Terrestrial New Zealand floras. Thirteen of the 56 genera reported from Mt Cook National Park (Wilson 1976) are shared with Mt Philistine. However, as will be shown, comparisons of lists of taxa identified only to genus level are of limited value. *Cyanothece* (=*Coccochloris*) *aeruginosa* is the only Mt Cook taxon, of 15 identified to species level, to be shared between the two studies. The two floras are generally dissimilar according to the information available, although this may partly be due to widespread appearance of certain taxa in cultures (such as *Pseudococcomyxa simplex* on agarised medium and *Cyanothece aeruginosa* in moist plate enrichments), and the examination of moss samples from Mt Philistine. Mosses were not collected in the Mt Cook study, and cultures were not used. The area over which samples were taken at Mt Cook was also much greater. However, all samples were taken east of the Main Divide, whereas Mt Philistine lies to the west and consequently has a higher rainfall, which may select a different community of algae. Other contrasting selective factors could include soil chemistry, irradiance, and the large amounts of glacial flour in streams, ponds, snow and air in the Mt Cook region. A paucity of xanthophyceans was recorded on Mt Philistine, which is common to the Mt Cook study, although it is unlikely that these would have been detected without the use of cultures.

The few other terrestrial algal floras recorded in New Zealand are mostly comprised of genus-only (and sometimes class-only) identifications. Considering, for example, that different species of *Chlamydomonas* may occur in an oligotrophic habitat

in New Zealand such as snow, or a eutrophic habitat such as oxidation ponds (personal observations), the validity of comparing genus-only lists is questionable.

A further difficulty associated with comparing species lists is its dependence on reliable identifications. The most detailed study of terrestrial algae in New Zealand, that of Everett (1998) in the Cass Basin, can be used to illustrate the importance of careful comparisons using descriptive information to assess their reliability, and the inadequacy of comparing lists of taxa identified to genus only in studies of widespread distribution.

According to the list of genera, 16 of 39 recorded from Cass are shared with the Mt Philistine flora. However, a more detailed examination shows that this is an overestimate. *Microcoleus* sp. differs from the Mt Philistine specimens due to pronounced indentations between cells. One of the trichome morphologies illustrated for *Oscillatoria* sp., not a shared genus, appears to include aerotopes, and is probably *Pseudanabaena* sp., which then becomes a shared genus. *Calothrix* sp. differs because its sheath is open at the tapered end, unlike the Mt Philistine specimens. The description of *Stigonema* sp. is missing, and this organism can be confused with *Fischerella* sp. which has been found near Cass (Croasdale and Flint 1972). *Chlorella* sp. contains a pyrenoid, in contrast to the 2 species recorded from Mt Philistine, and *Elliptochloris* sp. was very rare and no mention is made of two autospore types in the identification. The identification of this genus is therefore open to doubt. *Oocystis* sp. bears little resemblance to cf. *Oocystis minuta* from Mt Philistine, which may have thickenings at one (rarely both) of the poles. This feature is actually shared with *Scotiellopsis* sp. from Cass, which appears to have no visible ribs and only one polar thickening, unlike the Mt Philistine *Scotiellopsis terrestris*. *Cosmarium* sp., which has a smooth cell wall and no apical depression, and *Mesotaenium* sp., which is surrounded by concentric mucilage layers, are clearly distinct from the Mt Philistine species. If all these differences are taken into account, the maximum possible number of shared taxa between the two studies is seen to be 10, rather than 16, and other more subtle differences, not detectable in the absence of living material for examination, may distinguish these.

Therefore, an accurate understanding of the biogeography of these organisms can only be gained by careful comparison of living specimens from different sites. If living material cannot be obtained, descriptive data must be available. Electron microscopy and molecular techniques, may be required to confirm the identities of morphologically similar individuals. It is clearly of value for future comparisons to include descriptive

data with species lists, to take identifications to the most detailed level possible, and to indicate uncertainty where it exists.

CHAPTER 7.
CONCLUSIONS

7.1. Summary of results of investigations

Sixty-seven distinct taxa were identified from the alpine zone on Mt Philistine (Chapter 6). Of these, eight are thought to be obligate snow algae. A ninth snow alga, *Raphidonema nivale*, is regarded as facultative in snow (Fukushima 1963, Hoham 1971, 1973). However, it was never recovered from habitats other than snow on Mt Philistine (Chapter 3). Other algae found in snow were the cyanophytes cf. *Gloeocapsa*, *Cyanothece aeruginosa*, *Fischerella* sp., and cf. *Ammatoidea*, the chlorophytes *Stichococcus* cf. *bacillaris*, *Klebsormidium elegans*, and *K. flaccidum*, and the diatoms *Gomphonema parvulum*, *G. truncatum*, and *Nitzschia* sp. The diatoms were never recorded from elsewhere on the site and were almost certainly transported onto the snow from further afield (Chapter 5). The cyanophytes were very common in other habitats (Chapter 3) and their presence in snow was presumably the result of short-distance wind transport. Viability of these organisms was not demonstrated. However, the chlorophytes from snow samples all grew in cultures, proving their viability. This suggests that they may be capable of growth in this environment. However, there is no proof that growth occurs because they were never found in direct examination of snow samples.

The algal flora of Mt Philistine has many similarities with floras from elsewhere (Chapter 3), particularly Marie Byrd Land, Antarctica (Broady 1989a). It is less similar to that reported from Mt Cook National Park (Wilson 1976). No flora reported from elsewhere is identical to that found on Mt Philistine. This is most obvious in the snow algal community, which contains organisms found previously only in North America (*Chlainomonas kolii*, *Chloromonas* sp. 3) with one found previously only in Antarctica (*Chloromonas rubroleosa*). *Chloromonas* sp. 4 (=*Scotiella antarctica*) has been reported previously only from polar or sub-polar latitudes. Although this combination of species may seem surprising, it may also simply indicate that our understanding of their biogeography is far from complete.

Within the site, snow and *Andreaea* moss support distinct assemblages of algae compared to other habitats (Chapter 3). No algae were found on Mt Philistine which convincingly demonstrated growth in snow as well as in other habitats. Snow clearly exposes organisms to unique environmental conditions of high light intensities, desiccation, and low temperatures (Chapter 4). Water availability in Mt Philistine surface snow becomes amenable for extensive growth of *Chlainomonas kolii* during storms, and only in surface snow of the tarn in the middle basin. The combination of

lower light intensities, and higher liquid water content in this snow during storm conditions are important for growth. Without this ecological information, the presence of *C. kolii* in an alpine snowpack would seem anomalous compared with previous reports from North America, where it has been found only in forested areas (Hoham 1974a).

Clearly water availability has an indirect effect in determining growth of algae in other habitats. For instance, vegetation which provides habitats for algae grows in water courses rather than on exposed slopes, particularly in the middle and upper basins where there is minimal soil. Ohtani and Kanda (1987) concluded that water availability and nutrient supply for moss growth largely influence the presence of epiphytic algae around Syowa Station, Antarctica. The capacity of mosses for absorption of rainwater and its retention between gametophyte plants is probably important for growth of algae associated with *Andreaea mutabilis* on Mt Philistine. Outside the relatively moist microenvironment in a moss cushion, drying of exposed surfaces is rapid whenever rain ceases.

Environmental conditions select for distinct assemblages of algae in snow and *Andreaea* moss (Chapter 3). However, transfer between habitats occurs during windy conditions (Chapter 5). This is most obvious in the observation of material blown onto snow from elsewhere. Problems of interpretation are created by this transfer when presence / absence data is used. Firstly, it is usually difficult or impossible to ascertain whether wind-dispersed propagules become active members of the algal assemblages in habitats to which they are dispersed when presence / absence data is used. This is especially so for those organisms (including many chlorophytes) which are detected only by culture methods. Secondly, a number of ubiquitous species which occur in many habitats (e.g. *Cyanothece aeruginosa*, cf. *Gloeocapsa*, *Fischerella* sp., *Myrmecia* cf. *irregularis*), cause different samples to be distinguished by rare species. These effects reduce the sensitivity of procedures such as ordination, which are used to detect patterns in algal assemblages between different samples.

The only evidence of long-distance dispersal of propagules onto the site is the few species of diatoms collected in traps but not recorded in the Mt Philistine habitats. These diatoms have been reported from elsewhere in New Zealand. No marine forms were detected. All other algae found in aerobiota collectors (Chapter 5) were found in habitat samples taken from the site, but most of these probably have a far wider distribution, and some of their propagules could have derived from elsewhere. Airborne dispersal of the snow algae dominant at the study site appeared to be minimal; however,

this may partly be due to inadequacies in collection methods, as lofting seems the most likely explanation for disappearance of the *Chlainomonas* population during summer.

Dispersal data provides some evidence that unicellular, r-strategist, culturable algae populations grow rapidly early in summer (Chapter 5), perhaps as a response to high nutrient levels in snowmelt which irrigates their habitats (Chapter 4) during this period. Growing trichomes of cf. *Ammatoidea* and *Fischerella* sp. indicate that this period may also be important for slower-growing algae (Chapter 3).

Loss of cells from surface snow over time is an interesting effect common to both aerobiota (Chapter 5) and snow algae growing *in situ* (Chapter 4). This may be a physical process associated with the diurnal freeze-thaw cycle. Snow algae decreased in abundance in surface snow at night during a hard freeze (Chapter 4). During sustained north-westerly rain the snow does not freeze overnight, which may be a further reason why growth of snow algae occurs during storm conditions.

7.2. Relating results to initial hypothesis

Distribution and dispersal of alpine algae on Mt Philistine are more complex than hypothesised in the introduction (Fig. 1.1). Snow contained the most distinct assemblage of all habitats. *Chlainomonas kolii*, *Chloromonas* sp. 1-4, *Raphidonema nivale*, *Chromulina* cf. *elegans*, and Chrysophyceae sp. 1 were never found elsewhere. Therefore, no evidence was obtained to suggest that any of these algae are facultative in snow. Although snow and *Andreaea* moss appear to select distinct assemblages of algae, those supported by other habitats are very similar.

The hypothesis (Fig. 1.1) was inaccurate in suggesting that epiliths are the only algae exposed when most of the site is covered in snow, because *Andreaea* moss is able to colonise very small fissures in rock surfaces and is therefore also exposed. This could contribute to selection of a distinct assemblage of algae by *Andreaea*.

The unifying hypothesis (Fig. 1.1) suggested that abundance of aerobiota should increase during summer, as snowfields melt and more habitat area becomes exposed. In fact, a decrease in abundance of culturable algae later in summer was observed in aerobiota collectors. This may be related to the "r"-strategy of growth of the organisms, and the reliance of the populations on irrigation by snowmelt, rather than to a change in the amount of exposed habitat. The Frisbee sampling technique is not sensitive enough to detect sufficient numbers of the rare species which distinguish distinct communities for a link to the source habitat of propagules to be made. As an example of this,

dominant snow algae from the site, which represent a small component of algal biomass at the site overall, were never recorded in aerobiota, despite other evidence suggesting the occurrence of wind dispersal.

Finally, investigation of snow ecology showed that liquid water content and nutrient concentrations distinguish snow on the tarn surface, where growth of *Chlainomonas kolii* and *Chromulina* cf. *elegans* occurs, from snow in other areas of the site. This result supports the suggestion that, although widespread airborne dispersal may occur (see above), at least some species of algae require specific conditions to form blooms in the snow, and the majority of snow at the site is not suitable for this growth.

7.3. Further work

The complete classification of many organisms awaits further studies of their ultrastructure and molecular genetics (see Chapter 6, section 6.4.1). Many of the common cyanophytes, such as *Fischerella* sp., cf. *Gloeocapsa*, and cf. *Ammatoidea*, require isolation into culture for their complete characterisation. The proposed life cycle of the chlorophyte *Chlainomonas kolii* could be confirmed if the collared cells could be generated in culture.

More widespread collection of snow algae from tarn surface habitats would reveal whether assemblages present on Mt Philistine are typical of these conditions. Conditions in surface snow on the Mt Philistine tarn, where *C. kolii* grows most abundantly, have been shown to differ from those in other snowfields (see Chapter 4). *C. kolii* has not been found in the Mt Cook region, where blooms of snow algae dominated by *Chlamydomonas* sp. are most frequently observed (Thomas and Broady 1997). It appears, therefore, that conditions in alpine snowfields at Mt Cook and Arthur's Pass are different. Further chemical analyses of snow samples from both areas may reveal differences in nutrient content.

Algal assemblages in habitats other than snow differ between Mt Philistine and Mt Cook National Park (Wilson 1976). How typical, therefore, are Mt Philistine assemblages? Further sampling in areas of different environmental conditions, such as rainfall, geology, and soil types, would place the present study in broader context.

More effective investigation of distribution patterns on the site would require a means to distinguish reproductively active members of a particular assemblage from those merely dispersed to the site but unable to reproduce. Molecular probes could be used to distinguish active algae in the field (Nienow 1996).

The sources of propagules present in the aerobiota could not be determined in my study because the technique used was not sensitive enough to detect the relatively rare species characteristic of certain habitats. Possibly, a large number of jet spore samplers (Wynn-Williams 1992) automatically activated at higher windspeeds, and with solar panel recharge for batteries, would be sufficient. However, helicopter support or several experienced field assistants would be required due to the weight of the apparatus.

Observational ecology of snow algae on Mt Philistine has reached a stage where experimental studies are appropriate. Experimental establishment of tarn conditions in another area of snow, where blooms have not been recorded, would be a good test of the conclusions reached in my study. However, difficulties would include that: 1) this would need to be monitored over several seasons, 2) it may disturb the site unacceptably, and 3) continual monitoring would be very challenging for investigators under typical weather conditions.

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APPENDICES

Appendix 1. Correction for snow ablation

For cautionary comments on the application of this methodology, refer to Chapter 4, section 4.4.1.

Deriving an equation to relate total snow algae concentration (y) at a given depth (x) to the concentration in the surface 10 cm (a)

Because the equation will be used in a calculation involving mean cell concentrations, the mean concentrations in Fig. 4.3.19 are used to formulate the equation. Also, ranges of depth are not useful for formulating an equation to describe the relationship, so the mean cell concentration was used at the midpoint of each range (e.g. 0-10cm depth becomes 5 cm depth), giving the relationship shown in Fig. A.1.

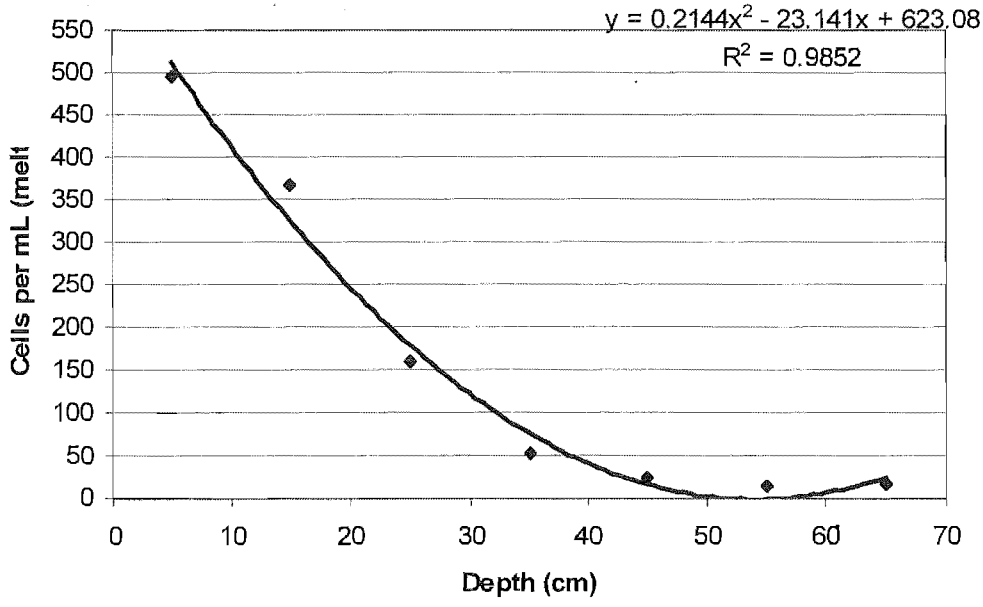

Fig. A.1. Relationship between depth in snow and total cell number, based on Fig. 4.3.19.

Equation 1 comes from the polynomial trendline fitted on Fig. A.1.

Eqn 1: $y = 0.2144x^2 - 23.141x + 623.08$

where y = cells per ml of snowmelt

x = depth (cm) in tarn snow

Eqn 1 describes the relationship between depth and cell number in melted tarn snow. This now needs to be described in terms of differing abundances in surface snow (since this is the information that will be used in the subsequent "correction" for snow ablation). This assumes that the same depthwise relationship holds true for different cell concentrations in the surface snow. The assumption can be tested using data from both seasons. For the moment, it is assumed that this assumption is true.

Different abundance in the surface 0-10 cm moderates the two coefficients and the y-intercept in Eqn 1. This moderation is calculable as follows. The y-value for x=5 cm in Fig. A.1. is 495. Since any surface abundance (=a) can be expressed as some factor of 495 then the two coefficients and y-intercept of Eqn 1 can be scaled by dividing by 495/a. Therefore:

$$\text{Eqn 2: } y = (0.2144a/495)x^2 - (23.141a/495)x + 623.08a/495$$
$$= (4.33a*10^{-4})x^2 - (4.67a*10^{-2})x + 1.26a$$

where a = cell concentration in the surface 0-10 cm of tarn snow.

The mean snow water equivalent measured over all sites in 1998 was 56% (n=28, standard error = 1.3). The low standard error implies stability, so this mean value is used to transform between cell concentrations in snow and snowmelt.

The validity of the depthwise relationship at different surface cell concentrations can be tested by applying Eqn 2 to surface (i.e. 5 cm) cell concentrations to generate predicted cell concentration values for 15 cm and then comparing them to known (counted) values obtained during the tarn study. This is set out in Table A.1 from 1999 data. This table shows that the predicted values agree well with the 10-20 cm cell concentration data.

Table A.1. Predicted cell concentrations at depth (x)=5cm using Eqn 2, compared with actual observed values as a test of validity of the ablation concentration correcting procedure.

Day of 1999 study period	Observed 0-10 cm abundance[1]	Predicted abundance[1] at 5 cm	Observed abundance[1] at 5 cm
0	536	352	377
4	231	152	208
6	346	227	225
8	242	159	218
10	332	218	202
12	265	174	160

[1] Cells ml^{-1}

Another test was made to determine if the relationship held for the 1998 data, as shown in Table A.2. These results show that when cell counts in the surface 10 cm are high (greater than about 500 cells/ml) the result is quite a large overestimate, suggesting that a second-order polynomial may not be an appropriate equation to express depth distribution in the 1998 data.

Table A.2. Repeat of the test in Table A.1 for 1998 data at depth (x)=35 cm.

Day of 1998 study period	Observed 0-10 cm abundance[1]	Predicted abundance[1] at 35 cm	Observed abundance[1] at 35 cm
17	142	22	20
19	118	18	18
24	198	31	16
30	754	118	11
54	1175	183	7

[1] Cells ml^{-1}

There are two considerations in deciding whether to retain Eqn 2 for the 1998 data:

1. An overestimate is preferable to an underestimate because it ultimately produces a conservative result when the predicted concentrations are used in ablation estimates.

2. Because the procedure uses cell concentrations at depth BEFORE the growth peak to calculate the correction, having to use high cell numbers (which generate the overestimates in Table A.2) is not a major problem.

Therefore, Eqn 1 was still deemed appropriate for the 1998 data.

Note that the equation is not valid after x = 55 cm, because the predicted values start to increase again; however observed abundances at 60-70 cm can be used as predicted values beyond this depth since:

1. The 1998 data always shows low values (less than 15 cells ml^{-1}) at 35 cm and 65 cm.
2. This is probably another overestimate because the trend in total cell numbers between 30 and 70 cm (shown in Fig. 4.3.19) is a further decrease.

Using the calculation

1999 data. The equation is unnecessary because the most snow depth lost between sampling days was 11 cm, and cell concentration to this depth is known for each sampling day.

The peak in cell numbers occurred on Day 9 of the data (i.e. increase occurred between Day 7 and Day 9). The relevant data for calculating ablation concentration of cells between these days is shown in Table A.3.

Table A.3. Relevant data for calculating ablation concentration of cells between days 7 and 9, 1999.

Day of 1999 study period	Mean cell concentration[1], tarn snow	
	0-10 cm	10-20 cm
7	536	377
9	1039	(not required)

[1] Cells ml^{-1}

The depth of snow loss over this period was 8 cm (Fig. 4.3.6).

Therefore the top 18 cm of snow on Day 0 contains the cells in the top 10 cm on Day 2 if cell increase is assumed to be entirely due to ablation concentration. Calculating this number requires conversion to a rectangular prism of snow (for convenience, of cross sectional area 1 cm^2). The number of cells in this rectangular prism 18cm deep on Day 0 is given by:

$$[536*0.56*10] + [377*0.56*8] = 4691 \text{ cells}$$

This number also represents the number of cells concentrated into the top 10 cm of snow by ablation by Day 2.

= 469 cells in 1 cm^3 (1 ml) of snow

= 469/0.56 = 1016 per ml of melt.

This number can now be compared with the observed number in the table above (=1039); thus we see, assuming no cell loss, that nearly all of the cell increase could theoretically arise from ablation of the snow since the previous sampling.

1998 data. Eqn 2 is required to repeat this procedure for the 1998 data because there is much more snow loss involved and the data available does not cover the cell numbers over all this depth.

The first peak in cell numbers in the 1998 season occurred between Days 27 and 30 (relevant data shown in Table A.4).

Table A.4. Relevant data for calculating ablation concentration of cells between days 27 and 30, 1998.

Day	Cell concentrations[1]		
	0-10 cm	10-20 cm	20-30 cm
27	89	58[2]	32[2]
30	753	(not required)	(not required)

[1] Cells ml^{-1}

[2] Calculated using eqn 2

16 cm of snow was lost during this period.

Therefore, the top 26 cm of snow on Day 27 contained the cells in the top 10 cm on Day 30. Using a rectangular snow prism of 1cm^2 cross section gives:

[89*0.56*10] + [58*0.56*10] + [32*0.56*6] cells in this snow.

= 931 cells in 10 cm^3 surface snow on Day 30

= 93 in 1 cm^3

= 93 per ml surface snow

= 93/0.56 = 166 per ml of melt.

Comparison with the tabulated value for surface snow on Day 30 (=753 per ml melt) show that some other factor(s) must be involved in the increase besides snow ablation.

The second major cell peak in the 1998 season occurred between Days 44 and 54 (relevant data are shown in Table A.5).

Table A.5. Relevant data for calculating ablation concentration of cells between days 44 and 54, 1998.

Day	Cell concentrations[1] at depths (midranges, cm):													
	5	15	25	35	45	55	65	75	85	95	105	115	125	135
44	101	66[2]	37[2]	15	4[2]	2[2]	2	2[3]	2[3]	2[3]	2[3]	2[3]	2[3]	2[3]
54	1175													

[1] Cells ml^{-1}

[2] Calculated using eqn 2

[3] Extrapolated from 60-70 cm data

Between Days 44 and 54, 126 cm of snow was lost.

Therefore the top 136 cm on Day 44 contains the cells in the top 10 cm on Day 54. So there is:

[101*0.56*10] + [66*0.56*10] + [37*0.56*10] + [15*0.56*10] + [4*0.57*10] + [2*0.57*10]*8 + [2*0.57*6] cells in the top 136 cm of snow on Day 44,

= 1347 cells in 10 cm^3 of 0-10 cm snow on Day 54

= 135 cells per ml snow

= 241 cells per ml melt.

Comparison with the tabulated value (1175 cells per ml) shows that this increase is emphatically due to more than just snow ablation, despite the depth of snow that was lost. (This peak corresponds to the decrease in NH_4-N recorded in the tarn snow between Days 47 and 54.)

Rate of Cell Loss from surface snow. If it is assumed that the apparent "stationary phases" of the population in both years (Fig. 4.3.14 days 14 to 27 and 33 to 47; Fig. 4.3.16 days 11-19) really correspond to a state when ablation concentration

(+growth, if any) equals cell loss (an assumption supported by the fact that ablation is always occurring, as shown by Fig. 4.3.5, 4.3.6), then Eqn 2 can be used to a theoretical rate of cell loss from the surface snow.

For the 1998 data, a stationary phase occurred between Days 14 and 27 (relevant data shown in Table A.6).

Table A.6. Relevant data for calculating loss of cells between days 14 and 27, 1998.

Day	Cells ml^{-1}				
	0-10 cm	10-20 cm	20-30 cm	30-40 cm	40-50 cm
14	156	102[1]	67[1]	6	1[1]
27	89				

[1] Calculated using eqn 2

Snow loss over this period was 42 cm.

In the surface snow on Day 14 (=surface 10 cm on Day 27) there were:

[156*0.56*10] + [102*0.56*10] + [67*0.56*10] + [6*0.56*10] + [1*0.56*2]

= 1855 cells in 10 cm^3 (in theory).

In reality there were 89*0.56*10 = 507.

Therefore there was a loss of 1348 cells in 13 days, = 104 cells per day, = 11.2/0.56

= 20 cells per ml melted surface snow per day.

Another stationary phase during the 1998 season occurred between Days 33 and 44 (relevant data shown in Table A.7).

Table A.7. Relevant data for calculating loss of cells between days 33 and 44, 1998.

Day	Cells ml^{-1}		
	0-10 cm	10-20 cm	20-30 cm
33	163	107[1]	59[1]
44	101		

[1] Calculating using Eqn 2.

Snow lost during this period was 22 cm.

In the top 21 cm on Day 33 (=top 10 cm on Day 44) there are:

[163*0.56*10] + [107*0.56*10] + [59*0.56*1] = 1545 cells in theory.

In reality there were 101*0.56*10 = 566 cells.

Thus there is a loss of 979 cells in 11 days, or 89 cells/day, =8.9/0.56 = 16 cells/ml melted surface snow per day.

This value compares well with the outcome of the first calculation.

The stationary phase in the 1999 data occurred from Day 11 to Day 19 (relevant data in Table A.8).

Table A.8. Relevant data for calculating loss of cells between days 11 and 19, 1998.\

Day	Cells ml^{-1}			
	0-10 cm	10-20 cm	20-30 cm	30-40 cm
11	231	209	84[1]	36[1]
19	266			

[1] Calculated using Eqn 2.

Between these days, 22 cm of snow was lost.

Therefore in the top 32 cm of snow on Day 11 (= top 10 cm of snow on Day 19) there were:

[231*0.56*10] + [209*0.56*10] + [84*0.56*10] + [36*0.56*2] = 2975 cells in theory.

In reality there are 266*0.56*10 = 1490 cells. Thus there is a loss of 1485 cells in 8 days, or 33 cells per ml of melted snow per day. This is slightly higher than the values calculated for the 1998 data.

Appendix 2. Standard curves for nutrient analyses

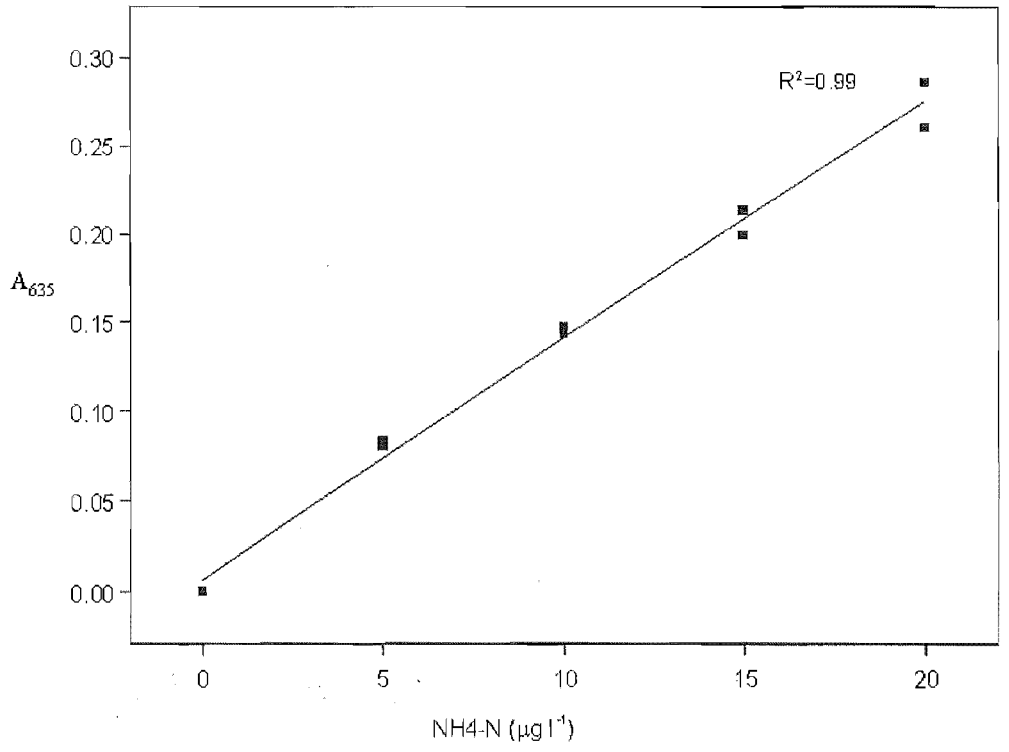

Fig. A.2. Standard curve for NH_4-N concentration vs absorbance at 635 nm according to the method of MacKereth *et al.* (1978).

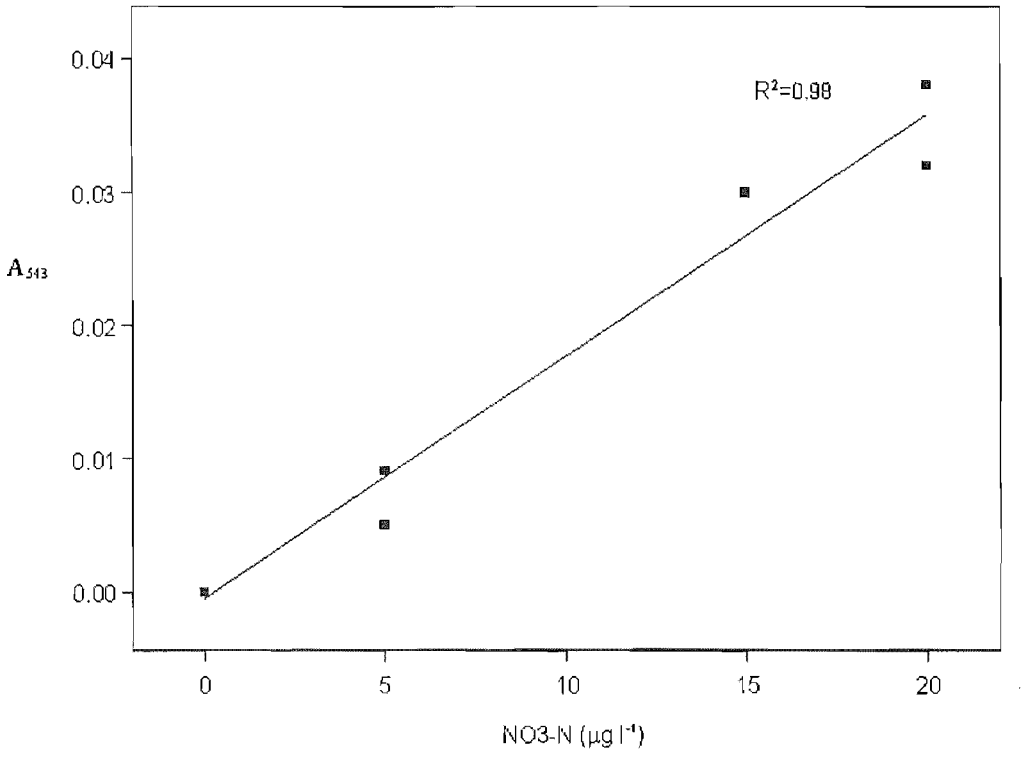

Fig. A.3. Standard curve for NO_3-N concentration vs absorbance at 543 nm according to the method of MacKereth *et al.* (1978).

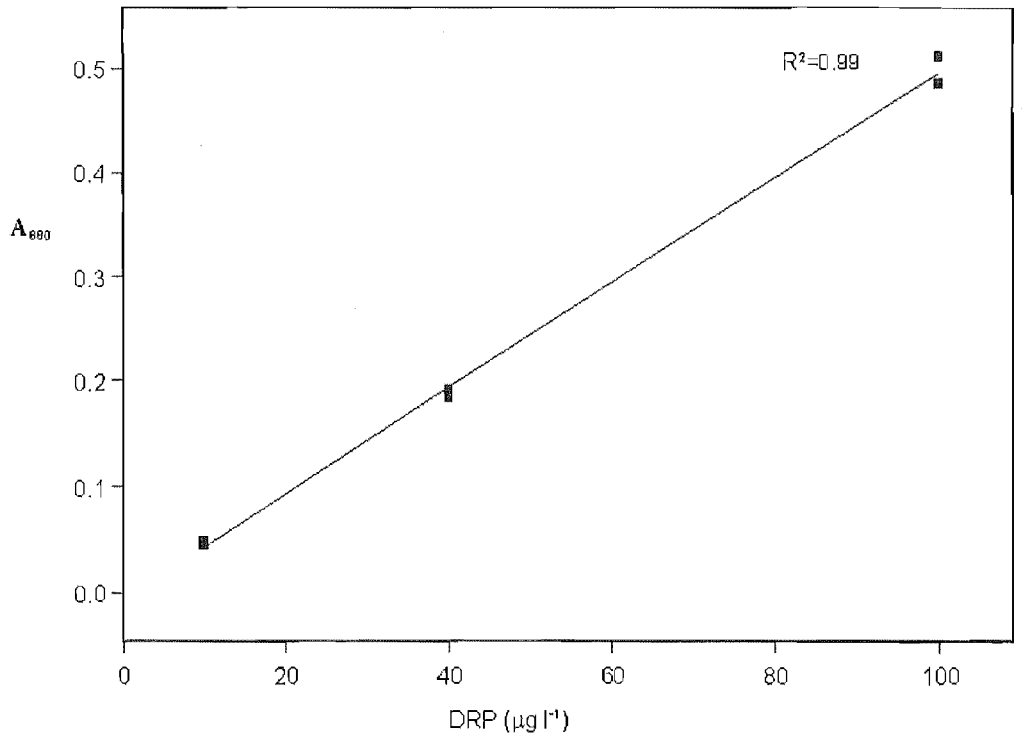

Fig. A.4. Standard curve for DRP concentration vs absorbance at 880 nm, according to the method of MacKereth *et al.* (1978).

Appendix 3. Tests for interference in nutrient analyses, using spiked samples

Table A.9. Results from analyses of standards, samples, and 1:1 mixes to test for interference in analyses. Comparison of theoretical and measured values for the mixtures indicates the reliability of the methods.

Solution	Theoretical concentrations ($\mu g\ l^{-1}$)	Measured in analysis ($\mu g\ l^{-1}$)
NH_4-N		
Standard	40.0	34.8
Sample	-	13.6
1:1 mix standard:sample	24.2	28.8
NO_3-N		
Standard	194.0	-[1]
Sample	-	3.0
1:1 mix standard:sample	98.5	125.3
DRP		
Standard	40.0	46.9
Sample	-	8.4
1:1 mix standard:sample	27.7	27.0

[1] Data missing . However, standard used was the same as that used undiluted in NO_3-N standard curve (see Appendix 2).